Bull. nat. Hist. Mus. Lond. (Zool.) **63**(1): 55–92 Issued 26 June 1997

Foregut anatomy and relationships of the Crassispirinae (Gastropoda, Conoidea)

YURI I. KANTOR AND ALEXANDRA MEDINSKAYA
A.N. Severtzov Institute of Animal Evolutionary Morphology and Ecology, Russian Academy of Sciences, Lenin Avenue 33, Moscow 117071, Russia
JOHN D. TAYLOR
Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

CONTENTS

Synopsis. The foregut anatomy of 31 species from the conoidean subfamily Crassispirinae is described. Great variation is found between species in the configuration of the foregut including features such as: the structure of the rhynchodeum, the morphology of the proboscis, the position and number of buccal tube sphincters, the position and structure of the buccal mass, the histology of the salivary glands and venom gland, the length of the oesophagus, the structure of the muscular bulb and the morphology of the radular teeth. Many species have marginal teeth of the wishbone type, but teeth are paddle-shaped in *Funa* and *Vexitomina*, harpoon-shaped in *Cheungbeia* and a hollow awl shape in *Ptychobela*. Many crassispirinae have rather similar shells, but different anatomies. Some species with similar radulae have different anatomies and others with similar anatomy have widely differing radulae. An analysis of relationships, using *Gemmula* as outgroup, shows that the various subgenera of *Crassispira* are not monophyletic and should be raised to generic status. Also, *Epidirona* is polyphyletic with some species belonging in the Turrinae, as do some species of *Turridrupa*. Additionally, some species classified in the genera *Guraleus*, *Antiguraleus* and *Paraguraleus*, until recently classified as Mangeliinae, belong in the Crassispirinae.

INTRODUCTION

Gastropods of the superfamily Conoidea are notable for the possession of a large, coiled venom gland, together with the highly modified radular teeth which are used to inject the venom into the prey. Although *Conus* is the most well-known taxon, it represents only a small part of the total diversity of the group which conservative estimates suggest as more than 4000 living species and 340 genera (Taylor, Kantor & Sysoev, 1993). Although most classifications (e.g. Powell, 1966; McLean, 1971) have been based largely on shell and radular characters, Taylor *et al.* (1993) have recently provided anatomical criteria, mainly derived from characters of the foregut, for the definition of suprageneric taxa of conoideans. Although their study involved anatomical investigation by serial sections of more than 72 species of conoideans, this nevertheless represented only a small fraction of the living genera and species. Moreover, amongst the species studied so far, a wide disparity in the configuration of the various organs of the foregut in the Conoidea has been revealed (Taylor *et al.*, 1993), with new arrangements still being discovered (Kantor & Taylor, 1994; Taylor, 1994; Kantor and Sysoev, 1996). These preliminary studies suggested that the subfamily Crassispirinae, one of four subfamilies of Turridae possessing 'wishbone' radular teeth, showed a wide variation in radular morphology and foregut anatomy, including the possibility of further evolutionary pathways to the hypodermic feeding system. Moreover, within the Crassispirinae, some species in the genera *Inquisitor, Funa* and *Ptychobela* which possess rather similar shells, were shown to have very different foregut and radular morphologies (Kilburn, 1989; Taylor, 1994; Taylor & Wells, 1994). The problem of using shell characters alone to classify conoideans has recently been highlighted in the case of the southern African species *Antiguraleus morgani,* previously classified in the Mangeliinae on the basis of shell morphology, but shown to be a likely crassispirinan on radular characters (Kilburn, 1994). For these reasons we decided to investigate the anatomy of the Crassispirinae in more detail.

Currently, some 48 genera and subgenera have been assigned to the Crassispirinae (Taylor *et al.*, 1993; Taylor & Wells, 1994; Kilburn, 1994) mainly on the evidence of radular characters, but in some cases on shell morphology alone. The subfamily is diverse in the tropical West America (McLean, 1971; Keen, 1971) with over 52 species recorded, and also in the Caribbean (Maes, 1983) and West Africa (Fernandes, Rolán & Otero-Schmitt, 1995). The Indo-Pacific fauna is less well known and there are many undescribed species, but Kilburn (1988; 1994) reports 54 species from Southern Africa, including numerous new genera and species, and many other species

Table 1 List of crassispirine gastropods and the outgroup *Gemmula* which have been sectioned, with details of their collection locations.

Crassispira (Crassispira) incrassata (Sowerby, 1834). North side of Venado Island, Panama, (8°53'N, 79°36'W). ANSP A9695 T357.
Crassispira (Crassispira) maura (Sowerby, 1834). Between Tortota and Venado Island, Bay of Panama, Republic of Panama (8°51'45N, 79°35'40W), 9–10 m, ANSP A9613 T357.
Crassispira (Gibbaspira) dysoni (Reeve, 1846). Isla de Lobos, Gulf of Mexico, Mexico (21°28'N, 97°13'W). ANSP A9423 T357.
Crassispira (Glossispira) harfordiana flucki (Brown & Pilsbry, 1913). Playa Benito, Campeche, Gulf of Mexico, Mexico (19°48'N, 90°36'W). ANSP 356707 A9734 T357.
Crassispira (?Crassispirella) latizonata (E.A. Smith, 1882). 1 km north of Holotown, St James, Barbados (13°11'N, 59°38'W). ANSP A9866G T357.
Crassispira (Monilispira) pluto Pilsbry & Lowe, 1932. West San Carlos Bay, Sonora, Mexico (27°57'N, 111°04'W). ANSP A9226 T357.
Crassispira (Striospira) kluthi Jordan, 1936. Venado Island, Panama (08°53'N, 79°36'W). ANSP 356323 A9698 T357.
Crassispira (Striospira) tepocana Dall, 1919. San Carlos, Guaymas, Sonora, Mexico, 35 m. ANSP A6670.
Crassispira (Striospira) xanti Hertlein & Strong, 1951. West side of Viradores sur, Bahia del Cocos, Costa Rica (10°34'45N, 85°43'35W). ANSP 35791A10167 T357.
Crassispira (Crassiclava) turricula (Sowerby, 1834). Off Nacascola, west side of Bahia Culebra, Bahia Culebra, Costa Rica (10°37'15N, 85°41'20W). ANSP A9753B T357.
Crassispira (Crassiclava) apicata (Reeve, 1845). Cactus Point, Prickly Pear Island, British Virgin Islands (18°30'55N, 64°22'30W). ANSP 355532 A9461E T357.
Burchia spectabilis Sysoev & Taylor, 1997. Houtman Abrolhos Islands, Western Australia (see Sysoev & Taylor, 1997). BM(NH).
Miraclathurella bicanalifera (Sowerby, 1834). West side of Viradores Sur, Bahia del Cocos, Costa Rica (10°34.30'N, 85°43.40'W). ANSP 357806 A9857A T357.
Hindsiclava andromeda (Dall, 1919). 3 miles southwest of Punta San Antonio, Sonora, Gulf of California, Mexico (27°54'N, 111°08'W). ANSP 358149 A10192G T357.
Hindsiclava militaris (Reeve, 1843) 2 miles east of Punta Doble, Sonora, Gulf of California, Mexico (27°55'N, 111°04'W). ANSP A10186 T357. West side of Bahia Culebra, off Nacascola, Bahia Culebra, Costa Rica (10°37'15N, 85°41'20W). ANSP 357487 A9753H T357.
Funa jeffreysi (Smith, 1875). South of Cape d'Aguilar, Hong Kong, 20 m. BM(NH).
Funa latisinuata (Smith, 1877). South of Cape d'Aguilar, Hong Kong, 20 m. BM(NH).
Ptychobela suturalis (Gray, 1838). North Lantau Island, Hong Kong, 12 m. BM(NH).
Cheungbeia mindanensis (Smith, 1877). South of Cape d'Aguilar, Hong Kong, 20 m. BM(NH).
Cheungbeia robusta (Hinds, 1839). South of Cape d'Aguilar, Hong Kong, 20 m. BM(NH).
Vexitomina garrardi (Laseron, 1954). 2–3 km E. of Malabar, Sydney, Australia (32°59.27'S, 150°16.48'E). AM.
Inquisitor cf *adenicus* Sysoev, 1996. Off Ras Madrakah, Oman (19°14.8'N, 56°26.8'E), 935 m. NMW.
Inquisitor aemula (Angas, 1877). Outer Lagoon, 10 m, Noumea, New Caledonia. BM(NH).
Inquisitor latifasciata (Sowerby, 1870). Off Cape d'Aguilar, Hong Kong, 25–30 m. BM(NH).
Epidirona gabensis (Hedley, 1922). 2 km East of Long Bay, Sydney, New South Wales, Australia, 66 m. AM.
Antiguraleus morganus (Barnard, 1958). Off Mendu Point 300 m, Transkei, South Africa (32°21.8'S, 29°0.0'E). NM.
Paraguraleus costatus (Hedley, 1922). 28 km east of south head of Little Bay, Sydney, NSW, Australia (33°58'54"S, 151°33'38"E), 183–192 m. AM.
Naudedrillia praetermissa (Smith, 1904). Off Sandy Point, Transkei, South Africa (32°37.4'S, 28°36.9'E), 90 m. NM.
Nquma scalpta Kilburn, 1988. Off Park Rynie, Natal, South Africa (30°23.2'S, 30°50.8'E), 140 m. NM.
Turridrupa bijubata (Reeve, 1843). 30 m, Beacon Island, Houtman Abrolhos Islands, Western Australia. BM(NH).
Haedropleura septangularis (Montagu, 1803). Torre San Giovanni, BR, Italy, 12 m. BM(NH).
Outgroup: subfamily Turrinae:
Gemmula deshayesii (Doumet, 1839). Off Cape d'Aguilar, Hong Kong, 20 m. BM(NH).

Abbreviations: AM, Australian Museum; ANSP, Academy of Natural Sciences, Philadelphia; BM(NH), Natural History Museum, London; NM, Natal Museum; NMW, National Museum of Wales.

are known from around the continental margins of the Indo-W. Pacific Ocean (Wells, 1994; Taylor & Wells, 1994; Sysoev, 1996). The relationships of the Crassispirinae to other conoideans are uncertain and those of the genera within the Crassispirinae are totally unknown; thus it is highly uncertain how the common genera of the East Pacific such as *Crassispira*, *Hindsiclava* etc. are related to some of the common Indo-W. Pacific genera such as *Inquisitor*, and *Funa*.

In order to establish the anatomical range of the Crassispirinae and evaluate characters which might be used to establish relationships both within the group and with other conoideans, we studied by serial sections the foreguts of 35 species. These were collected within the East Pacific, Caribbean, Mediterranean and Indo-Pacific provinces from a wide variety of habitats ranging from intertidal to abyssal depths. Additionally, we used *Gemmula deshayesi* (subfamily Turrinae) as an outgroup. This is the most extensive comparative study yet attempted of the anatomy of any group of Conoidea.

MATERIAL AND METHODS

Details of all the species used in the study are listed in Table 1. For all species longitudinal serial sections were made of the foregut, cut at 8 μm and mostly stained in green Masson's trichrome. Radulae were cleaned with a dilute sodium hypochlorite solution and examined by SEM.

ANATOMICAL DESCRIPTIONS

Abbreviations used in the anatomical figures

asg	acinous salivary gland
asgm	modified acinous salivary gland
bc	buccal cavity
blp	buccal lips
blpi	invertible buccal lips
bm	buccal mass
bs	buccal sac
bt	buccal tube
bts	buccal tube sphincter,
btsa	anterior sphincter of the buccal tube
btsi	intermediate sphincter of the buccal tube
cf	circular fold, surrounding opening of buccal sac
cfbt	circular fold of the buccal tube
con	circumoesophageal nerve ring
ct	connective tissue of the buccal mass wall
ctl	connective tissue layer of the muscular bulb
ebt	sac-ike enlargement of the buccal tube
ep	epithelial pad
gre	glandular part of the rhynchodeum
iep	invaginated epithelium of the proboscis tip
ipt	inverted proboscis tip
ire	non-glandular invertible part of the rhynchodeum
lmb	lumen of the muscular bulb
mebt	thickened muscular wall of sac-like enlargement of buccal tube
ngre	non-glandular non-invertible part of the rhynchodeum
oe	oesophagus
oel	oesophageal loop
p	proboscis

pt proboscis tip
rh/rhc rhynchocoel
rhs rhynchostomal sphincter
rs radular sac
rst rhynchostome
rtsg anastomosing tubular salivary gland
rw rhynchodeal wall
rwg rhynchodeal wall glandular
sd salivary duct
se sac-like enlargement of buccal tube
sg salivary gland
stag single tube acinous salivary gland
t radular tooth.
tsg simple tubular salivary gland
v valvule
vg venom gland
vga duct of venom gland

In this section we describe and illustrate the foregut anatomy and radulae of each of the species examined. The terminology of the anatomical characters and organs largely follows Taylor *et al.*, (1993). Most of the features are illustrated diagrammatically in Fig. 1, with details of others given in the descriptions of individual species.

Crassispira (Crassispira) incrassata (Sowerby, 1834)

(Figs 2, 4a)

Rhynchodeum and proboscis

The rhynchostomal sphincter is large and located in a slightly posterior position. The epithelium of the posterior rhynchodeal wall is continuous with that of the proboscis wall for slightly more than half the length of the rhynchodeum. Extremely large proboscis retractor muscles are attached to the rhynchodeum at the border between the two different epithelia and at the proximal ends to the columellar muscle.

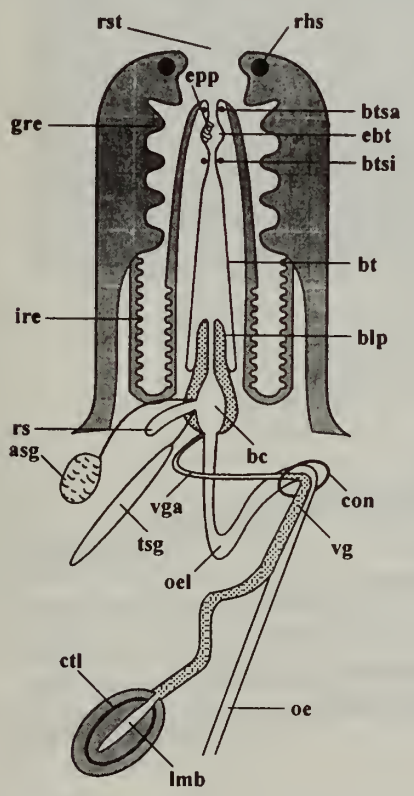

Fig. 1 Composite diagram of the foregut of a hypothetical crassispirine gastropod, showing the location of the major structures discussed in the text. No single species has all these structures.

The proboscis is long (more than half of the rhynchodeum), slightly narrowing towards the tip. The proboscis tip is not inverted inside. The muscles of the proboscis wall in the posterior two thirds of the proboscis are significantly thicker than in the anterior section. The proboscis lies coiled within the rhynchocoel (shown uncoiled in drawing to illustrate relative proboscis length). There are two anterior buccal tube sphincters. A sac-like enlargement of the buccal tube is present, with the epithelium lining it taller than that of the rest of the tube. An epithelial pad is also present. There is no intermediate buccal tube sphincter.

The proboscis walls and posterior part of the rhynchodeum are highly folded, suggesting significant elongation of the proboscis during protraction. The proboscis wall is thick, comprising about 10% of proboscis diameter in the posterior half. In the anterior one third of the proboscis, the wall is thinner, but due to the decrease in proboscis diameter the wall comprises about 12% of the total diameter. The wall of the buccal tube is also thick, comprising about 7% of proboscis diameter in its posterior half. Small buccal lips are present.

Buccal mass and oesophagus

The large and very long buccal mass is located entirely within the proboscis, with a thick wall and is curved. The oesophagus is elongated between the buccal mass and nerve ring. The buccal sac is very short.

Glands

The salivary glands are very large and acinous, protruding nearly to the anterior of the rhynchodeum. The histology of the venom gland changes abruptly before passing through the nerve ring. The duct of the venom gland is ciliated, and opens into the buccal cavity at the posterior border with the oesophagus. The muscular bulb is large, with thick walls formed from two equal layers of circular muscle fibres separated by a connective tissue layer, with a third much thinner innermost layer of larger circular fibres.

Odontophore and radula

The odontophore is medium-sized, consisting of a pair of unfused cartilages, formed by single layer of cells. The radula (Fig. 4a) consists of marginal teeth of the robust wishbone type, with a thick, distally-pointed major limb and a shorter, thinner minor limb. The marginal tooth is short, ca.180μm (0.5% of SL (shell length),1.2% AL (aperture length)).

Crassispira (Crassispira) maura (Sowerby, 1834)

(Figs 3, 4b)

Rhynchodeum and proboscis

The rhynchodeal sphincter is medium-sized and anteriorly located. The epithelium of the anterior two thirds of the rhynchodeum is glandular, but posteriorly, it changes abruptly to low, cubic non-glandular, epithelium, which is continuous with that of the proboscis wall. The anterior rhynchodeum is narrow with high folds.

The proboscis is short, occupying less than half the length of the rhynchodeum, with the proboscis tip not inverted. The proboscis walls are rather thick, forming about 20% of the proboscis diameter, but the walls of the buccal tube are thin, composing about 4% of the total diameter. The mouth is narrow. The muscles of the proboscis

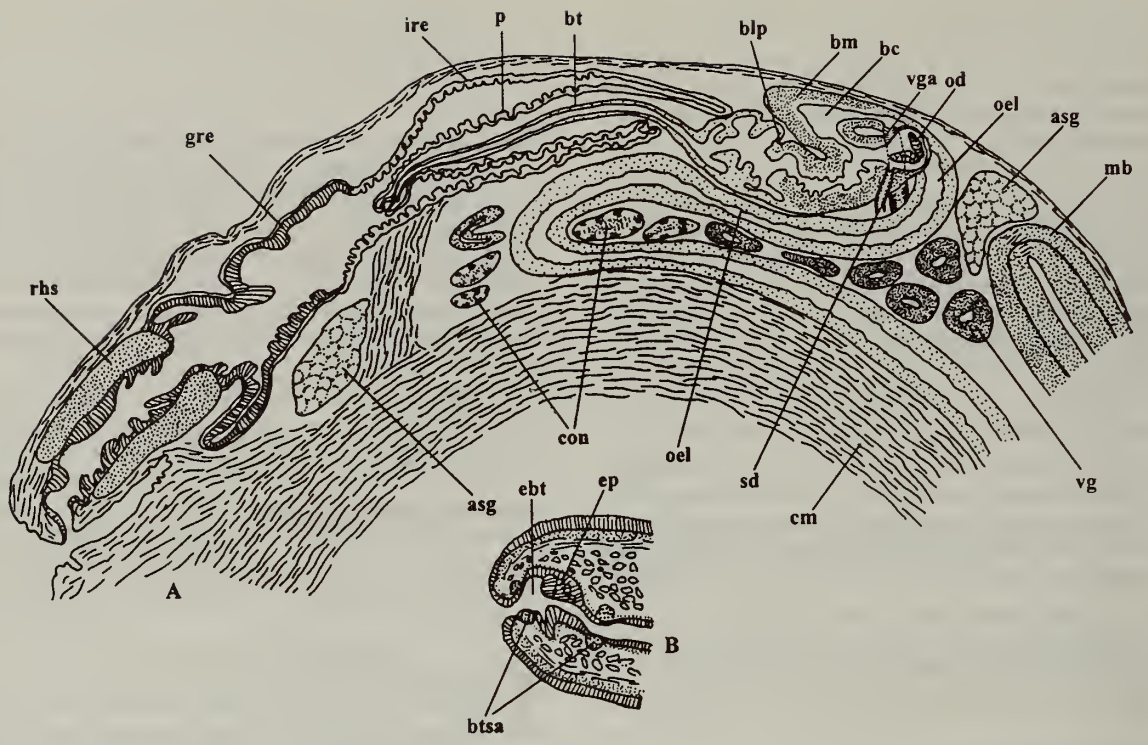

Fig. 2 *Crassispira (Crassispira) incrassata* (Sowerby, 1834). A, semidiagrammatic longitudinal section of the foregut (only one salivary duct is shown); B, longitudinal section of the proboscis tip.

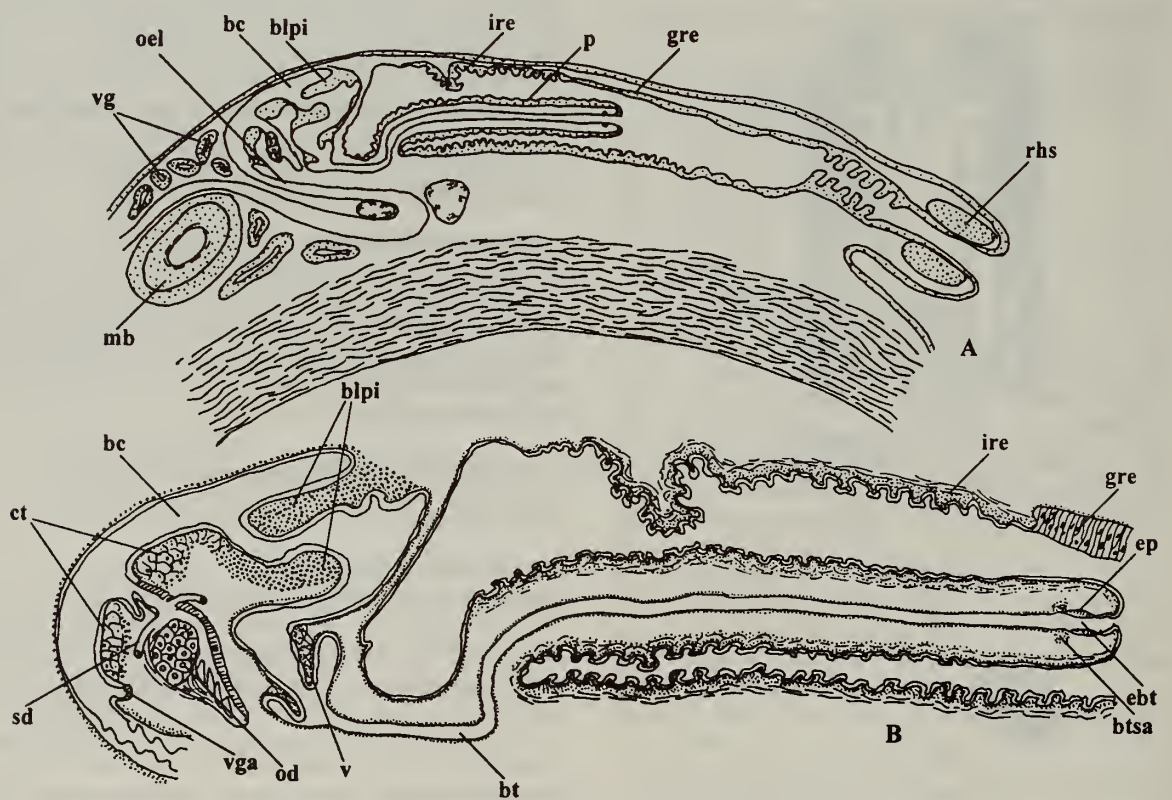

Fig. 3 *Crassispira (Crassispira) maura* (Sowerby, 1934). A, semidiagrammatic longitudinal section of the foregut (salivary glands and ducts not shown); B, longitudinal section of the proboscis and buccal mass.

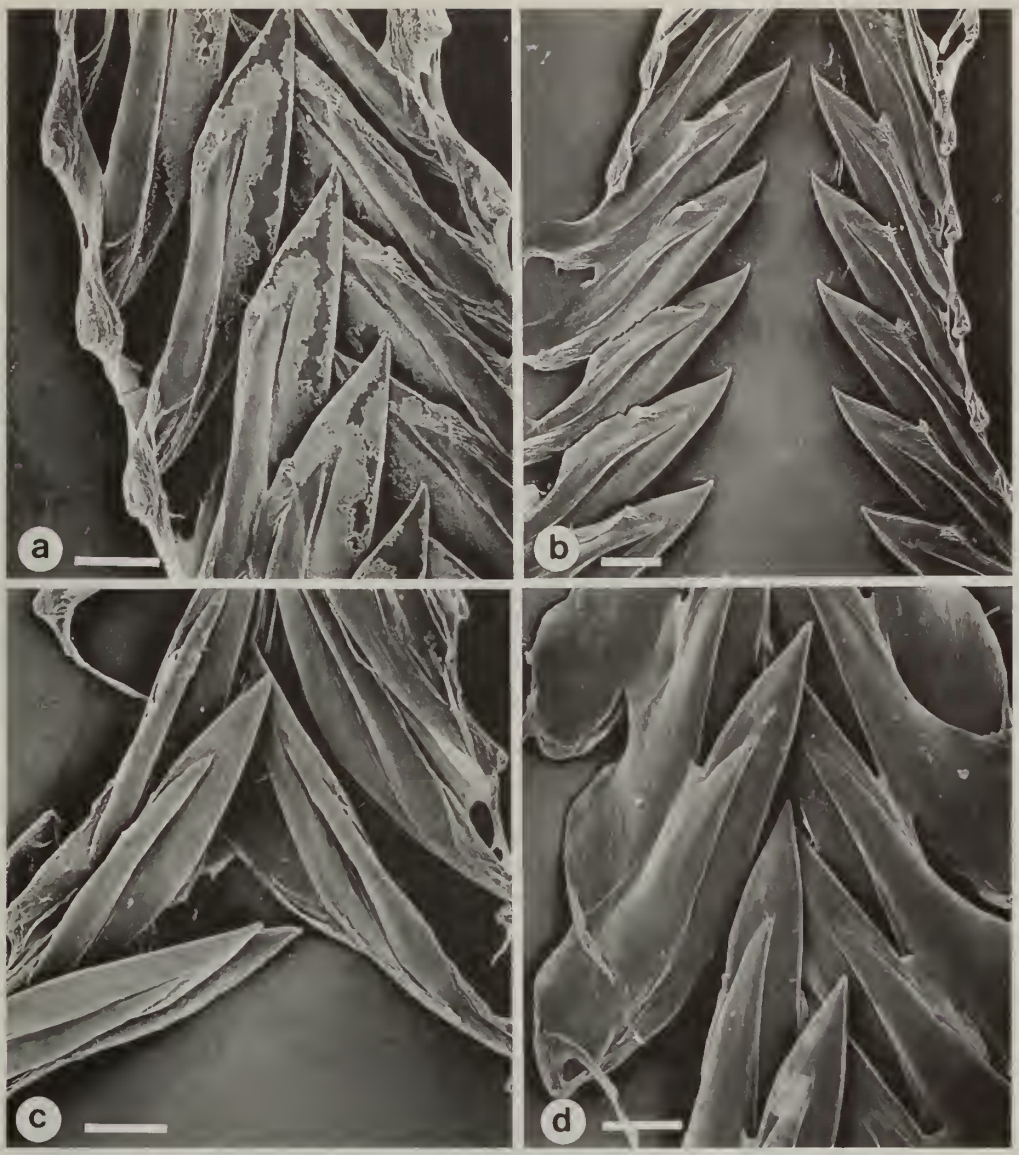

Fig. 4 Radulae of Crassispirinae. a, *Crassispira (Crassispira) incrassata* b, *Crassispira (Crassispira) maura* c, *Crassispira (Gibbaspira) dysoni* d, *C. (Glossispira) harfordiana flucki*. Scale bars = 20μm.

walls are equally developed along its length. There is a small anterior buccal tube sphincter, positioned at the base of the small sac-like enlargement of the buccal tube, which also has an epithelial pad. An intermediate buccal tube sphincter is absent. The buccal tube is very narrow, both inside the proboscis and for some distance behind it, and lined with a very low epithelium. Some distance behind the proboscis, the buccal tube expands greatly and forms two small, poorly-muscularized lips which are directed anteriorly, similar to the 'valvule.' (Sheridan *et al.* 1973). The buccal lips are large and muscular, with the dorsal one inverted inside the buccal cavity.

Buccal mass and oesophagus

The buccal mass is medium-sized and situated to the posterior of the proboscis base. Its dorsal wall is very thin. By contrast, the ventral wall near the entrance of the radular diverticulum is thick, but formed mainly by a layer of loose connective tissue, which is 4–8 times thicker than the muscle layer. The oesophagus is greatly elongated between the buccal mass and nerve ring, forming a long loop. The buccal sac is of medium length and narrow.

Glands

The salivary glands are very large and acinous, with ducts that are thick and coiled, but become very thin as they approach the buccal mass. The venom gland changes in histology after passing anteriorly through the nerve ring. The duct of the gland is narrow, unciliated, and opens just to the posterior of the buccal cavity. The muscular bulb is large, with most of the wall formed by two subequal layers of longitudinal muscle fibres, divided by a connective tissue layer, with a third innermost, thin layer of circular muscle fibres.

Odontophore and radula

The odontophore is medium-sized with paired, unfused cartilages. The radula consists of only marginal teeth of the wishbone type, with the major limb robust, solid and pointed with a long straight leading edge. The minor limb is smaller and thinner, but tapers towards the base (Fig. 4b). The marginal tooth is short, ca.130μm (0.3% of SL, 1.0% AL).

Crassispira (Gibbaspira) dysoni (Reeve, 1846)

(Figs 4c, 5)

Rhynchodeum and proboscis

The rhynchostomal sphincter is medium-sized and anteriorly located. The epithelium of the anterior half of the rhynchodeal wall is tall and glandular, while the posterior half is continuous with that of the proboscis wall. The proboscis tip is not inverted. The proboscis is short (about half of the rhynchocoel), not coiled, but slightly folded and narrowing towards the tip. The muscles of the proboscis wall are equally developed along its length.

The anterior buccal tube sphincter is small, whilst the sac-like enlargement of the buccal tube is long, with a long epithelial pad, formed of large cubic cells with large nuclei. At the base of the enlargement, there is an intermediate sphincter, which lies at a distance of three radular tooth lengths from the mouth. The walls of the sac-like enlargement are thicker than the rest of the buccal tube and similar to those of *C. (Crassiclava)* spp. The buccal tube is lined with ciliated epithelium. The proboscis wall is thin, forming about 10% of the proboscis diameter, while the wall of the buccal tube comprises about 7% of proboscis diameter. Buccal lips are absent.

Buccal mass and oesophagus

The buccal mass lies to the posterior of the proboscis, and is small, thin-walled and curved, and comprises less than one fifth of the proboscis length. The oesophagus is greatly elongated between the buccal mass and nerve ring and forms a long loop. The epithelium bears very long cilia, which occupy nearly the whole lumen. The opening of the radular diverticulum into the buccal cavity is quite narrow and bordered by a rather tall circular muscular fold, similar to that seen in *C. harfordiana*. The salivary ducts open into the radular sac at the base of this fold (Fig. 5).

Glands

The salivary glands are large and acinous, with ducts that are thick, very long and highly coiled. The histology of the venom gland changes after passing anteriorly through the nerve ring. The duct of the gland is narrow, highly coiled and probably ciliated. The gland itself is very long, thick, and occupies a large part of the body haemocoel. The muscular bulb is large, with thick walls formed of two equal layers of circular muscle fibres, divided by a connective tissue layer. The lumen of the bulb is filled with venom granules.

Odontophore and radula

The odontophore is small, consisting of paired, unfused, subradular cartilages, formed by a single layer of cells. The radula consists of marginal teeth (Fig. 4c) which are of the wishbone type, with a large, solid, sharply pointed, major limb and a shorter, slender, secondary limb. The marginal tooth is medium long, ca.105μm (0.8% of SL, 1.8% AL).

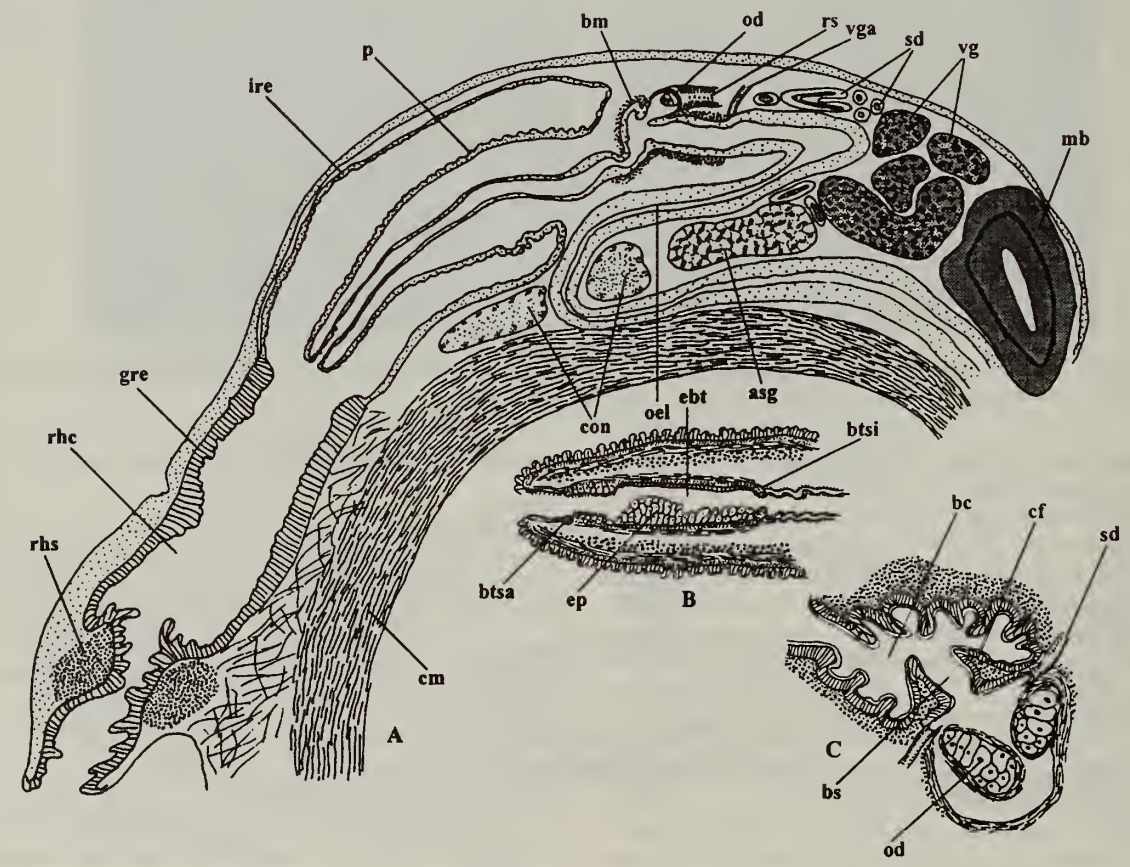

Fig. 5 *Crassispira (Gibbaspira) dysoni* (Reeve, 1846). A, semidiagrammatic longitudinal section of the foregut (salivary ducts not shown); B, longitudinal section of the proboscis tip; C, section of the buccal mass showing the opening of the radular sac.

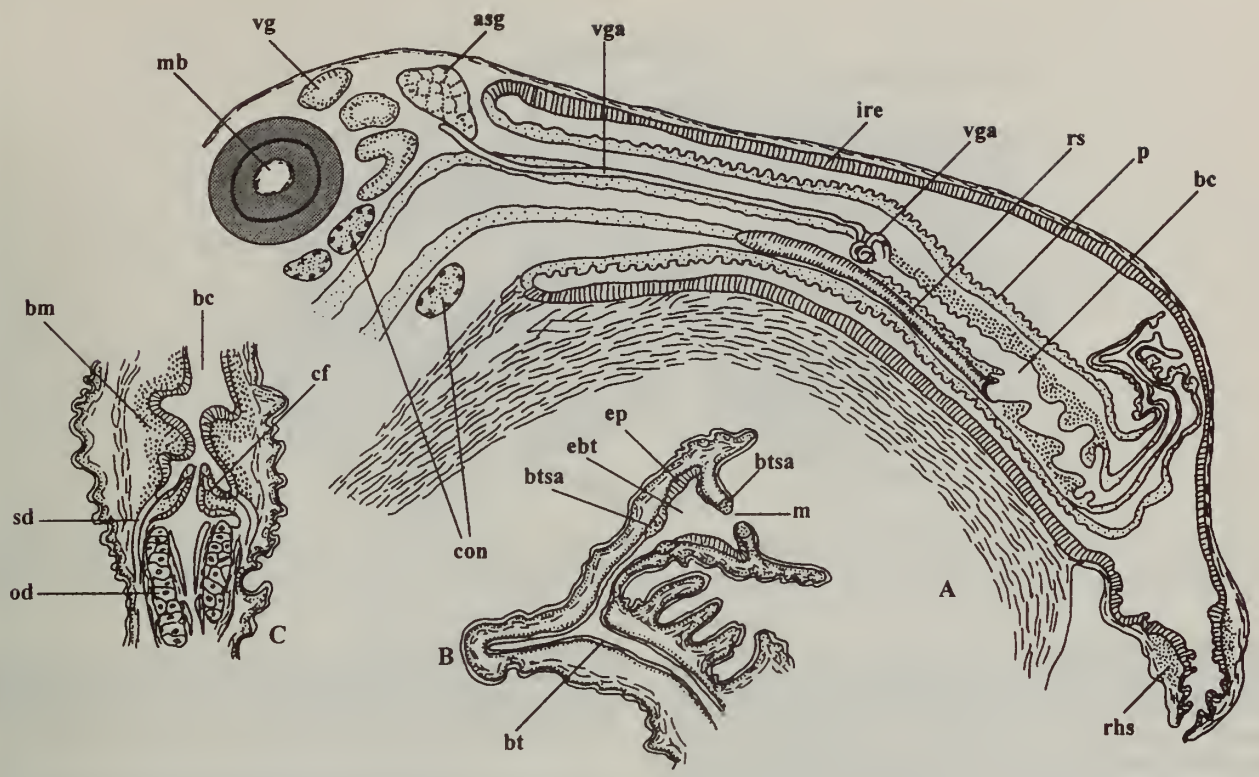

Fig. 6 *Crassispira (Glossispira) harfordiana flucki* (Brown & Pilsbry, 1913). A, semidiagrammatic longitudinal section of the foregut (salivary glands not shown); B, longitudinal section of the proboscis tip; C, section of the buccal mass, showing the opening of the radular sac.

Crassispira (Glossispira) harfordiana flucki (Brown & Pilsbry, 1913)

(Figs 4d, 6, 30e)

Rhynchodeum and proboscis

The rhynchostomal sphincter is small and slightly posteriorly situated. The epithelium of the rhynchodeum wall is glandular and that of the posterior rhynchodeal wall is not continuous with that of the proboscis wall. The proboscis tip is not inverted. The proboscis is very long and highly coiled (longer than the rhynchocoel and shown uncoiled in Fig. 6). The muscles of the proboscis wall are equally developed along its length, except at the very anterior.

The anterior part of the proboscis from the mouth opening to the buccal mass is very thin (about 0.1 mm compared to the proboscis length of about 5–6 mm) and highly folded. The proboscis tip is highly expanded to form a wineglass-shaped structure (Fig. 6, 30e). Closer to the tip, there is a septum with a small, circular sphincter surrounding the narrow opening. The septum delimits the sac-like enlargement of the buccal tube. The epithelium lining this is significantly taller than that of the rest of the tube, forming a low epithelial pad. At the base of the enlargement, there is a second small sphincter. Pieces of one, or possibly more, marginal teeth (fragmented during sectioning) were seen attached to the epithelium. The distance between the two sphincters corresponds to about one tooth length. It is possible, that the enlargement serves as a storage area for detached marginal teeth. There is no intermediate sphincter in the buccal tube.

Buccal cavity and oesophagus

The buccal mass is long (equivalent to about one quarter of proboscis length), with moderately thick walls and no curvature. It is contained entirely within the proboscis and starts within the distal third of the proboscis length. The walls of the buccal cavity form several annular folds. The buccal lips are small.

The oesophagus is highly elongated between the buccal mass and nerve ring, but because the buccal mass is located anteriorly within the proboscis, there is virtually no loop. A buccal sac is absent. The opening of the radular diverticulum into the buccal cavity is narrow and bordered by a rather tall circular muscular fold. The salivary ducts open into the cavity at the base of this fold (Fig. 6).

Glands

The salivary glands are small, paired and acinous and lie at the proboscis base. The ducts are highly coiled. The histology of the venom gland changes abruptly after passing through the nerve ring. The duct of the venom gland is unciliated, narrow, and highly coiled before opening into the buccal cavity at the border with the oesophagus. The muscular bulb is large, with thick walls formed of two layers of longitudinal muscle fibres, separated by a connective tissue layer, with a much thinner innermost layer of larger circular fibres

Odontophore and radula

The odontophore is small and composed of a pair of unfused cartilages formed by a single layer of cells. The radula consists of marginal teeth of the wishbone type (Fig. 4d), with a solid, pointed, curved major element and a shorter and narrower secondary element. The marginal tooth is medium long, ca.195µm (0.7% of SL, 2.7% AL).

Crassispira (Crassispirella) latizonata (E. A. Smith, 1882)

(Fig. 7)

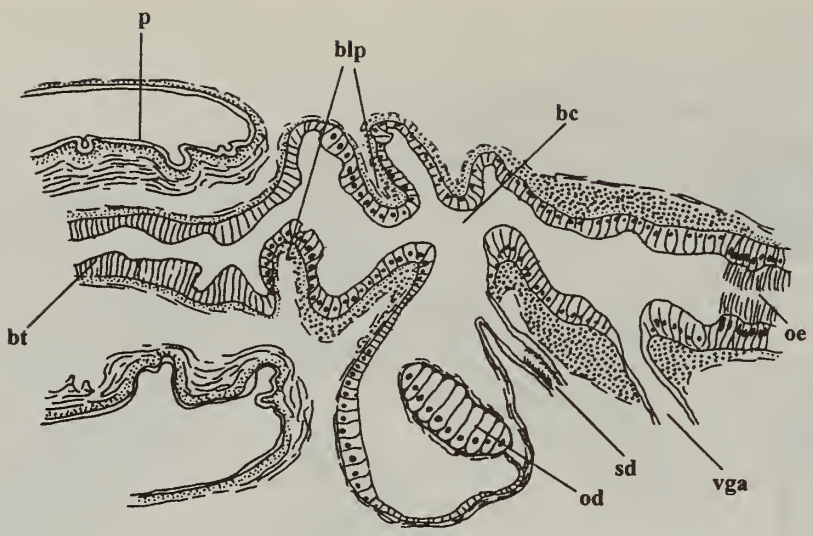

Fig. 7 *Crassispira (Crassispirella) latizonata* (Smith, 1882). Longitudinal section of the posterior part of the proboscis and buccal mass (only one salivary duct is shown).

Rhynchodeum and proboscis
The rhynchostomal sphincter is small and anteriorly located. The epithelium of the anterior half of the rhynchodeal wall is glandular, arranged into high folds, but to the posterior it is continuous with that of the proboscis wall. The dorsal wall of the proboscis tip is inverted inside. The proboscis is medium long (about half of the rhynchocoel) and not coiled. The muscles of the proboscis wall are equally developed along its length.

There is a small, anterior buccal tube sphincter, which lies in front of the well developed, sac-like enlargement of the buccal tube, lined with tall epithelium. There is no epithelial pad. A large, intermediate sphincter of the buccal tube is present, which lies at the base of the distal enlargement at a distance of about 2.5 radular tooth lengths from the mouth opening. The proboscis walls are not thick, composing about 15% of proboscis diameter. The wall of the buccal tube wall is also not thick, forming about 8% of proboscis diameter. Small buccal lips are present.

Buccal cavity and oesophagus
The buccal mass lies posterior to the proboscis base and is large, equivalent to about one quarter of proboscis length. Anterior to the opening of the radular sac, the walls of the buccal cavity are thin, similar to those of the buccal tube, but become thicker to the posterior.

The oesophagus is greatly elongated between the buccal mass and nerve ring and forms a very long loop. A remarkable feature of the oesophagus is that its epithelium bears very long cilia which occupy the whole lumen. The duct of the radular sac is broad and rather long. The buccal sac very short.

Glands
The salivary glands are tubular in histology, coiled and situated near the nerve ring. The salivary ducts are very long, coiled and thick. The histology of the venom gland changes abruptly after passing through the nerve ring. The duct of the venom gland is ciliated, coiled and narrow, with the same diameter as the salivary ducts, and opens into the buccal cavity at the border with the oesophagus. The muscular bulb is large, with thick walls formed of two layers of longitudinal muscle fibres, divided by a connective tissue layer, with a much thinner, innermost layer of circular fibres.

Odontophore and radula
The odontophore is rather large and consists of paired subradular cartilages, formed by single layer of cells. The radula was not examined and there are, unfortunately, no published illustrations.

Crassispira (Monilispira) pluto Pilsbry and Lowe, 1932

(Fig. 11a)

Rhynchodeum and proboscis
The rhynchostomal sphincter is large and anteriorly situated. The epithelium of the anterior seven eighths of the rhynchodeal wall is tall, glandular and arranged into high folds, while that of the posterior one eighth is continuous with the proboscis wall. The proboscis tip is not infolded. The proboscis is very long (ca 1.5 times longer than rhynchocoel), coiled in the anterior part and thick. The muscles of the proboscis wall are more developed at the base.

An anterior buccal tube sphincter is present. The sac-like enlargement of the buccal tube is present, but not well differentiated. Also, there is an epithelial pad with a marginal tooth attached to it. An intermediate sphincter is absent. The proboscis walls are thick, comprising about 20% of proboscis diameter, whilst the buccal tube wall is medium-thick, forming about 15% of the total diameter. The buccal lips are large and muscular.

Buccal mass and oesophagus
The buccal mass lies posterior to the proboscis, is rather long, with thick walls, uncurved and equivalent to about half the proboscis length. The oesophagus is elongated between the buccal mass and nerve ring and forms a long loop. The buccal sac is very short.

Glands
The salivary glands are large and acinous. The histology of the venom gland changes after passing the nerve ring. The duct of the venom gland is narrow and unciliated. The gland itself is long. The muscular bulb was unfortunately missing from the sections.

Odontophore and radula
The odontophore is large, consisting of paired, unfused, subradular cartilages, formed by a single layer of cells. The radula consists of

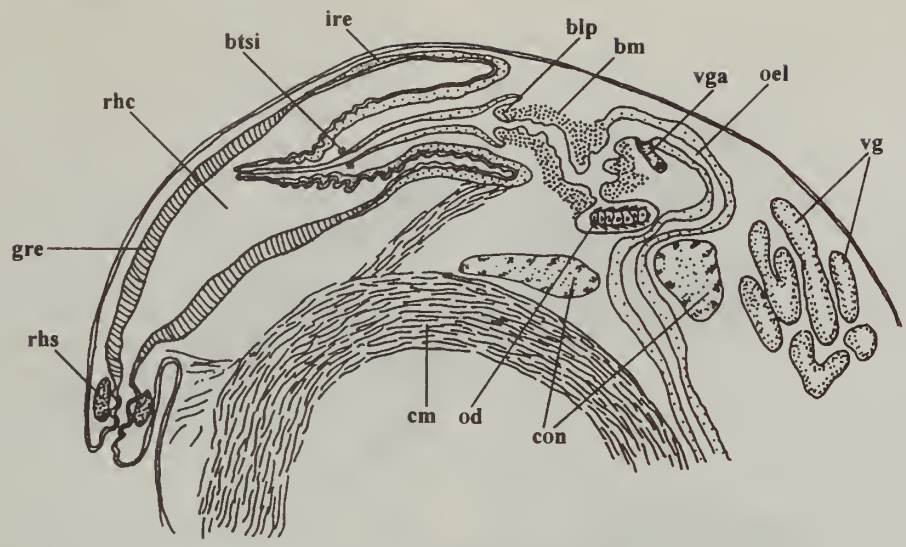

Fig. 8 *Crassispira (Striospira) tepocana* Dall, 1919. Semidiagrammatic longitudinal section of the foregut (salivary ducts and glands not shown).

marginal teeth of the wishbone type (Fig. 11a), with a solid, sharply-pointed major limb and a shorter, slender, secondary limb. The marginal tooth is long, ca.175µm (1.1% of SL, 2.9% AL).

Crassispira (Striospira) tepocana Dall, 1919

(Fig. 8)

Rhynchodeum and proboscis
The rhynchostomal sphincter is small and anteriorly located. The epithelium of the anterior two thirds of the rhynchodeal wall is tall and glandular, while that of the posterior one third is continuous with the proboscis wall.

The proboscis is short (about half of the rhynchocoel), coiled and folded in its anterior part, becoming narrow towards the tip. The muscles of the proboscis wall are better developed at the base. The proboscis tip is not infolded. There is no anterior buccal tube sphincter and the sac-like enlargement of the buccal tube is slight. The anterior part of the buccal tube is very narrow. There is a very small intermediate sphincter, which lies at a distance of about three radular tooth lengths from the very narrow mouth opening. The proboscis wall is thick, composing 25% of proboscis diameter at its base, and about 16% in its apical part. The buccal tube wall is medium-thick, making up about 10% of proboscis diameter. The buccal lips are very small.

Buccal mass and oesophagus
The buccal mass is long and curved and lies posterior to the proboscis, equivalent to about two thirds of proboscis length. The oesophagus is elongated between the buccal mass and nerve ring and forms a short loop. The epithelium bears very long cilia, which occupy nearly the whole lumen. The duct of the radular sac is broad and very short, whilst the buccal sac is virtually absent.

Glands
The salivary glands are medium-sized, with the ramified tubular morphology. The histology of the venom gland changes abruptly anterior to the nerve ring. The duct of the venom gland is narrow and unciliated. The gland itself is very long and occupies a large part of the body haemocoel. The muscular bulb is extremely large, with thick walls formed of two subequal layers of longitudinal muscle fibres, divided by a connective tissue layer, with a much thinner innermost layer of circular muscle.

Odontophore and radula
The odontophore is medium-sized, with paired, unfused subradular cartilages, formed by a single layer of cells. The radula is illustrated by McLean (1971, fig. 66) and consists of marginal teeth of the wishbone type (similar to *C. kluthi*, Fig. 11b), with a large, robust and pointed major limb and a thinner, secondary element which is attached near the tip of the major limb.

Crassispira (Striospira) kluthi Jordan, 1936

(Fig. 11b)
The foregut anatomy of this species is similar to that of *C. tepocana* and only the differences are listed below.

The rhynchostomal sphincter is larger and located further to the posterior. The rhynchodeum is entirely glandular with no change in epithelium along its length. The proboscis is highly coiled. The proboscis walls are very thin in the anterior part and are thinner than in *C. tepocana* (about 15 % of the proboscis diameter). The buccal mass lies within the proboscis base. The oesophagus is more greatly elongated and coiled between the buccal mass and nerve ring. The duct of the venom gland is very long and highly coiled. The radular teeth (Fig. 11b) have a large, pointed, major limb and a more slender secondary limb which is attached near the tip of the major limb. The marginal teeth are short, ca.90µm (0.5% of SL, 1.4% AL).

Crassispira (Striospira) xanti Hertlein & Strong, 1951

(Fig. 9)

Rhynchodeum and proboscis
The rhynchodeal sphincter is large and anteriorly located. The epithelium of the anterior half of the rhynchodeum is glandular and arranged into high folds; posteriorly, this changes abruptly to a non-glandular epithelium, which is continuous with that of the proboscis wall.

The proboscis is short, about half of the rhynchodeum length, with the tip not infolded. The proboscis walls are thick, composing

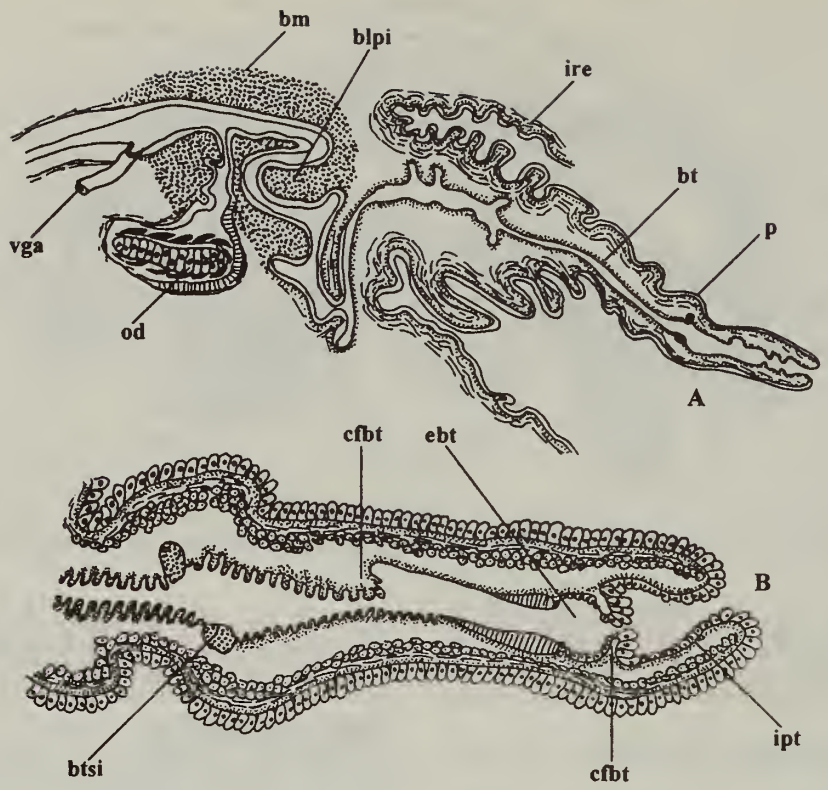

Fig. 9 *Crassispira (Striospira) xanti* Hertlein & Strong, 1951. A, longitudinal section of the proboscis and buccal mass (salivary ducts not shown): B, longitudinal section of the proboscis tip.

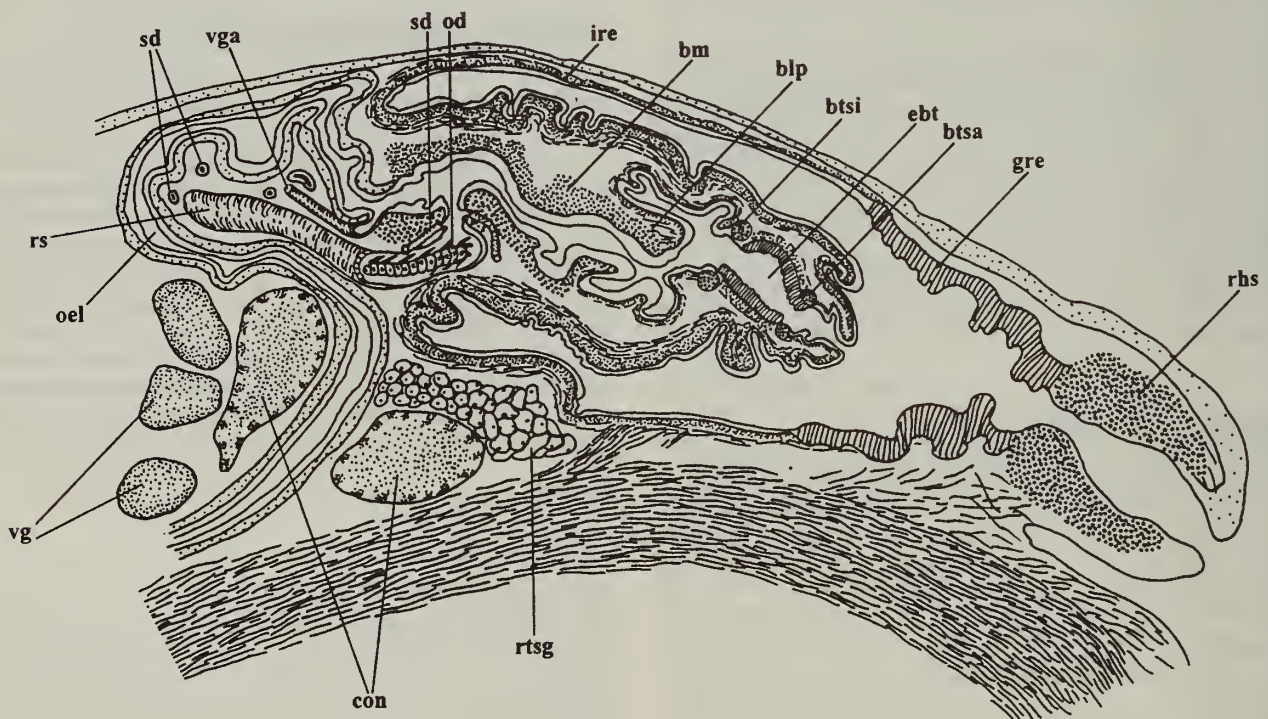

Fig. 10 *Crassispira (Crassiclava) turricula* (Sowerby, 1834). Semidiagrammatic section of the foregut.

about 25% of proboscis diameter, whilst the buccal tube walls are highly folded, but thin, making up about 6% of the total diameter. The mouth is narrow. The proboscis is highly folded, with the base more muscular than the tip. Both the anterior buccal tube sphincter and the epithelial pad are absent. The sac-like enlargement of the buccal tube is long and lined with tall epithelium, but poorly differentiated from the buccal tube. It has two unequal circular folds. The anterior one is larger and directed anteriorly and lined with tall epithelium. To the posterior of the second fold, the wall of the buccal tube forms an invagination, where the base of the radular tooth is situated. The intermediate sphincter of the buccal tube is rather large. The buccal tube is lined with a low, loose epithelium and after leaving the proboscis it expands slightly in diameter and forms two small, poorly-muscularized lips which are directed anteriorly, similar to the 'valvule' seen in Mangeliinae (Sheridan *et al.,* 1973). The buccal lips are medium-sized, muscular, with the dorsal one inverted inside the buccal cavity.

Buccal mass and oesophagus
The buccal mass is situated to the posterior of the proboscis, is rather large and muscular, with a narrow lumen, and sharply curved. The oesophagus is greatly elongated between the buccal mass and nerve ring, forming a long loop. The buccal sac is long and narrow.

Glands
The salivary glands are medium-sized and acinous, with long, coiled and rather thick ducts. The venom gland changes in histology after passing through the nerve ring, but its diameter remains nearly the same and there is no defined duct. The gland opens into the oesophagus just posterior to the buccal cavity. The muscular bulb is large, composed of two layers of longitudinal muscle fibres, divided by a connective tissue layer, with an innermost, thin layer of circular muscle fibres.

Odontophore and radula
The odontophore is medium-sized, with paired unfused cartilages formed of one layer of cells. The radula illustrated by McLean (1971, fig. 67) is composed of marginal teeth of the wishbone type, with a robust and pointed major limb and a smaller, shorter, secondary limb.

Crassispira (Crassiclava) turricula (Sowerby, 1834)

(Figs 10, 11c–d)

Rhynchodeum and proboscis
The rhynchostomal sphincter is large and anteriorly situated. The epithelium of the anterior one third of the rhynchodeal wall is glandular, and arranged into high folds; whilst the posterior two thirds is continuous with that of the proboscis wall. The proboscis tip is formed by the invagination of the outer proboscis wall into the buccal tube. This is confirmed by the similar, low, cubic epithelia of the outside of the proboscis and the anterior-most part of the buccal tube. Posteriorly in the buccal tube the cubic epithelium is replaced by one with columnar cells.

The proboscis is of medium length (little more than half of the rhynchocoel), uncoiled, but with telescopically folded walls. The muscles of the proboscis wall are better developed at its base.

An anterior buccal tube sphincter is present. The sac-like enlargement of the buccal tube is well-defined and lined with tall, glandular epithelium. An intermediate sphincter is also present, situated at the base of the sac-like enlargement. The walls of the buccal tube in the area of the enlargement are much thicker and formed by relatively thicker circular muscle fibres, as if this part of the tube is capable of strong contraction. The proboscis wall is thick, composing about 25% of proboscis diameter, whilst the wall of the buccal tube is medium-thick, representing about 5% of proboscis diameter. Large muscular buccal lips are present.

Buccal mass and oesophagus
The buccal mass lies mainly within the proboscis and is very long, equivalent to about two thirds of the proboscis length. The oesophagus is greatly elongated between the buccal mass and nerve ring and forms a long loop. It is narrow and lined with an epithelium bearing long cilia. The duct of the radular sac is broad and rather long. The buccal sac is short.

Glands
The salivary glands are large, with the ramified tubular morphology. The salivary ducts are very long, coiled, and thick. The histology of the venom gland changes anterior to the nerve ring. The duct of the venom gland is narrow and unciliated. The muscular bulb is extremely large, with thick walls mainly formed of two layers of longitudinal muscle fibres, separated by a connective tissue layer, with a much thinner, innermost layer of circular fibres.

Odontophore and radula
The odontophore is large, consisting of paired, unfused, subradular cartilages, formed by a single layer of cells. The radula (Figs 11c–d) consists of both lateral and marginal teeth. The lateral teeth (use of the term 'lateral' teeth here does not imply homology with the lateral teeth of other neogastropods) are low and arcuate, sharply-curved anteriorly towards the midline of the ribbon. In profile these teeth are cuesta-like, with steep anterior faces and gentle posterior slopes. The marginal teeth are of the robust wishbone form with a large, pointed, major element and a thinner, shorter, minor element. The marginal teeth are ca 200μm long (0.6 %SL; 2.0%AL)

Crassispira (Crassiclava) apicata (Reeve, 1845)

(Fig. 12)

The anatomy of the foregut is similar to the preceding species and only the differences are mentioned.

The anterior part of the rhynchodeum, which is lined with glandular epithelium is shorter than in *C. turricula* and comprises about half the length of the rhynchodeum. The proboscis walls do not form telescopic folds. Also, the proboscis is longer and occupies about two thirds of the rhynchocoel. Only the anterior buccal tube sphincter is present and an epithelial pad is located within the sac-like enlargement of the buccal tube. The enlargement itself is shorter than in *C. turricula*. The proboscis walls are much thinner and comprise only about 6% of its diameter. The salivary glands are very large with the ramified tubular morphology. The radula (from Maes, 1983 figs 31 & 37) consists of both lateral and marginal teeth. The lateral teeth have the arcuate form illustrated for *C. turricula* (Figs 11c–d), whilst the marginal teeth have the wishbone form with a robust major limb and a shorter, thinner, minor limb.

Hindsiclava andromeda (Dall 1919)

(Fig. 13)

Rhynchodeum and proboscis
The rhynchostomal sphincter is of medium size and located slightly to the posterior. The epithelium of the anterior half of the rhynchodeal wall is tall and glandular, whilst the posterior is low and cubic and

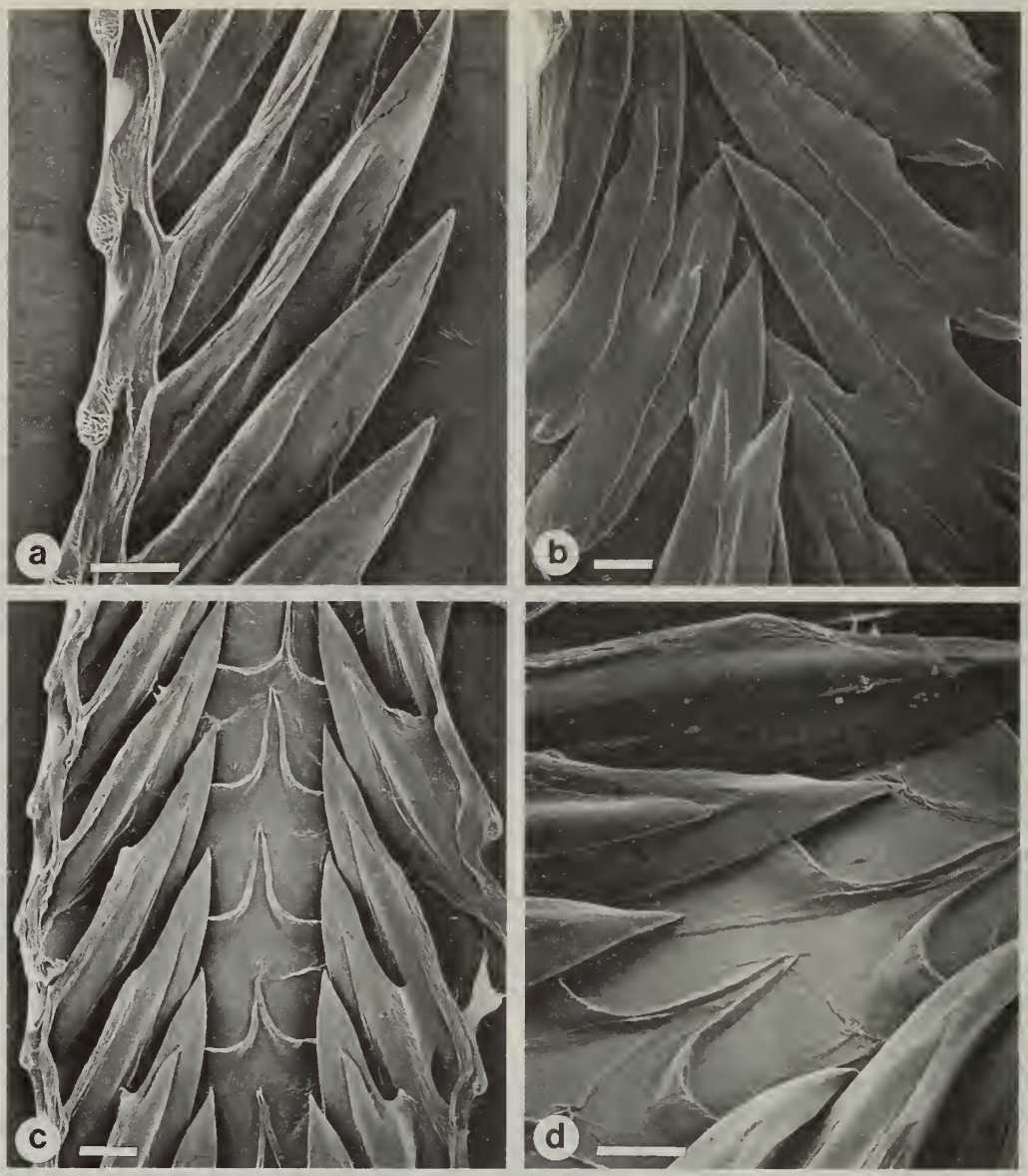

Fig. 11 Radulae of Crassispirinae. a, *Crassispira (Monilispira) pluto*, scale bar = 20μm b, *Crassispira (Striospira) kluthi* scale bar = 10μm c, *Crassispira (Crassiclava) turricula* scale bar = 30 μm d, *C. (C.) turricula* scale bar = 20 μm.

continuous with that of the proboscis wall. The wall of the rhynchodeum in its posterior part is muscular and free and much thicker than to the anterior. This posterior part of the rhynchodeum is able to evert. Powerful retractor muscles are attached at the point where the rhynchodeal epithelium changes; these run along the rhynchodeum and are attached to the buccal mass.

In the retracted position, the proboscis is rudimentary (Fig. 13), being only about twice as long as than the radular tooth length. The mouth opening is very narrow. There is no anterior buccal tube sphincter and the sac-like enlargement of the buccal tube is small. At the base of the enlargement there is an intermediate sphincter, which lies at a distance of about three radular tooth lengths from the mouth and posterior to the proboscis. The buccal tube forms a loop posterior to the proboscis and widens greatly before opening in the buccal mass.

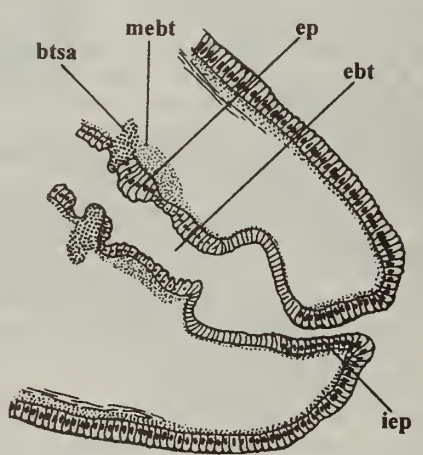

Fig. 12 *Crassispira (Crassiclava) apicata* (Reeve, 1845).

Buccal mass and oesophagus

The buccal mass is medium-sized, and located to the posterior of the

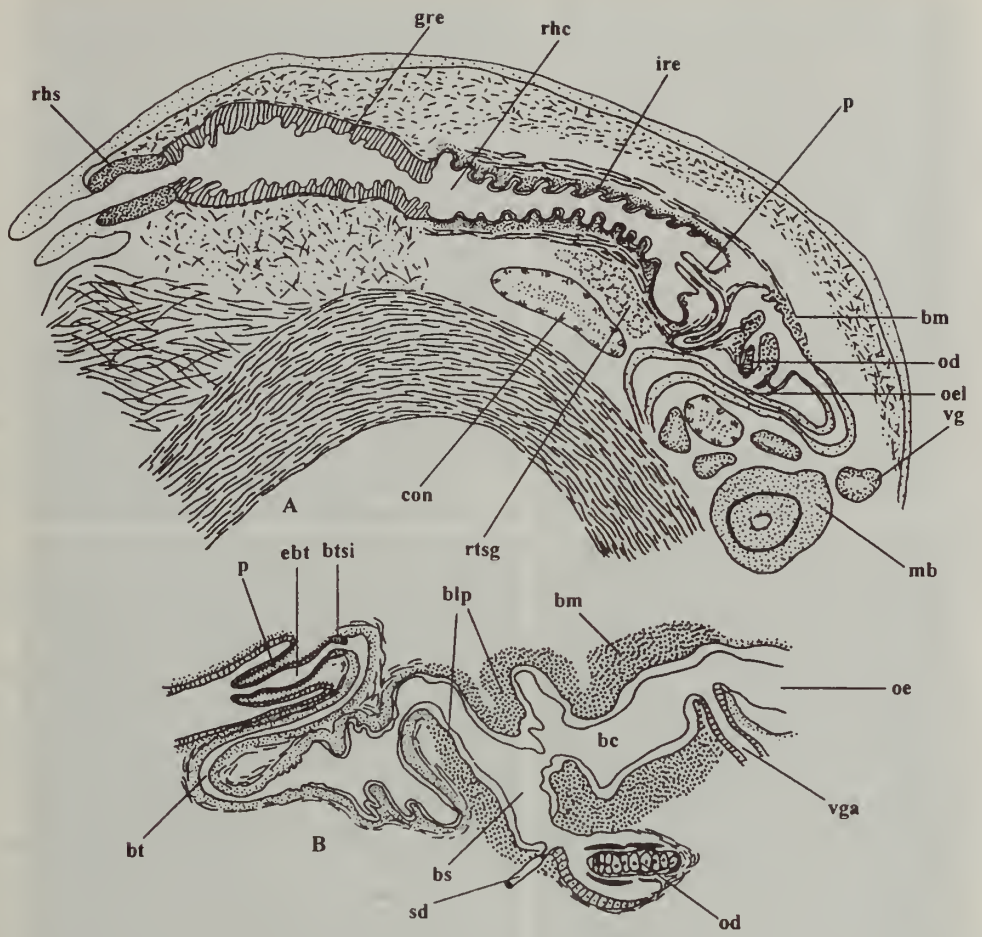

Fig. 13 *Hindsiclava andromeda* (Dall, 1919). A, Semidiagrammatic longitudinal section of the foregut (salivary ducts not shown); B, longitudinal section of the proboscis and buccal mass (only one salivary duct is shown).

proboscis. It has rather muscular walls and is not curved. The buccal lips are asymmetrical, the ventral lip being large, and the dorsal medium-sized. The oesophagus is greatly elongated between the buccal mass and nerve ring and forms a long loop. The opening of the radular diverticulum into the buccal cavity is narrow, and the salivary ducts open at the entrance of radular diverticulum into the buccal mass. A buccal sac is absent.

Glands

The salivary glands are very large with the ramified tubular morphology. The salivary ducts are very long and thick, but only slightly coiled. The histology of the venom gland changes abruptly soon after passing anteriorly through the nerve ring. The duct of the venom gland is narrow, coiled and unciliated. The muscular bulb is large, with a narrow lumen and thick walls mainly formed of two equal layers of longitudinal muscle fibres, divided by a connective tissue layer, with a thin, innermost layer of circular fibres.

Odontophore and radula

The odontophore is small, consisting of a pair of unfused, subradular cartilages, formed by a single layer of cells. Unfortunately, no radular information is available for this species, but it is presumed to be similar to *Hindsiclava militaris* (see below).

Hindsiclava militaris (Reeve, 1843)

(Figs 14 a–b)

Two specimens were sectioned. The species is very similar in general foregut anatomy to *H. andromeda* and differs mainly in the slightly longer proboscis (which occupies from 1/7 to 1/5 of the rhynchodeum). The proboscis is very muscular, with the entire lumen filled with retractor muscles. The anterior buccal tube sphincter is very small, and hardly visible. The proboscis tip is invaginated. This is confirmed by the change of the epithelium in the anterior part of the buccal tube. A short buccal sac is present.

Radula

The radula consists mainly of two rows of marginal teeth. These are wishbone in form but have a very distinctive, hairpin-like morphology (Figs 14 a–b). The major limb is elongate and pointed, slightly concave-upwards in profile with raised edges. The secondary limb is long and slender, attached to the major limb near the tip but detached and distantly separated for most of the length, with separate attachment to the radular membrane. Another feature of the radula is the regular low, transverse ridges which cross the central part of the ribbon (Fig. 14a) The marginal teeth are medium long, ca.140μm (0.5% of SL, 1.9% AL).

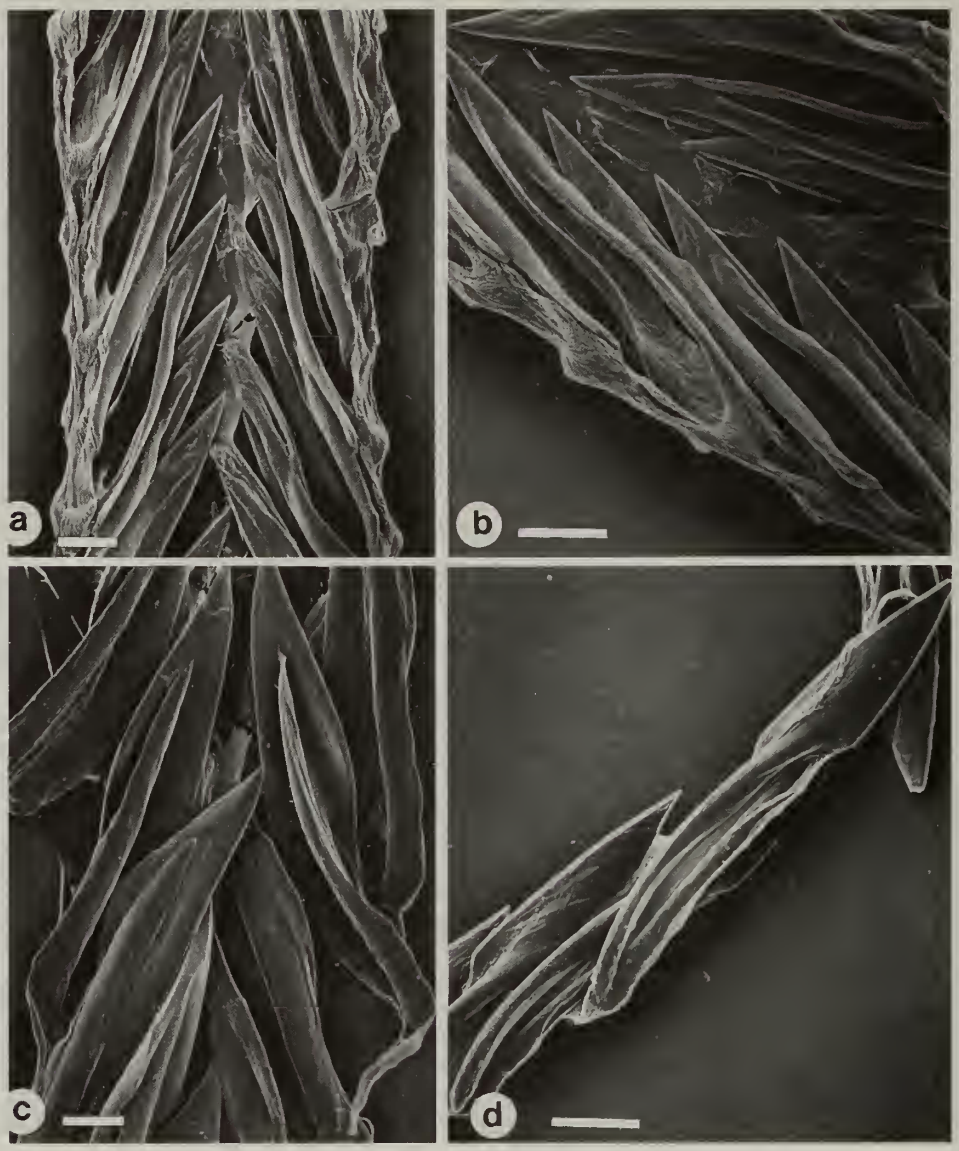

Fig. 14 Radulae of Crassispirinae a, *Hindsiclava militaris* b, *H. militaris* c, *Miraclathurella bicanalifera* d, *Haedropleura septangularis*. Scale bars = 20μm.

Miraclathurella bicanalifera (Sowerby, 1834)

(Fig. 14c)

Rhynchodeum and proboscis

The rhynchodeal sphincter is small and anteriorly located. The epithelium of the anterior part of the rhynchodeal cavity is glandular, whilst that of the posterior rhynchodeum is low, non-glandular, and continuous with that of the proboscis wall The rhynchostome is rather wide.

The proboscis is as long as the rhynchodeal cavity, highly folded, and very thick at the base, but sharply narrowing towards the tip. The proboscis walls are thick and form about 22% of the proboscis diameter at its base. The wall muscles at the proboscis tip are much thinner. The proboscis is very muscular and its lumen is mostly filled with the retractors. The mouth is narrow. The anterior buccal tube sphincter is absent. The sac-like enlargement of the buccal tube is poorly defined, but lined with taller epithelium with a small epithelial pad. There is a large intermediate sphincter, situated approximately one third of the distance down the proboscis. The buccal tube is very narrow anteriorly, but broad in the posterior part of the proboscis. Its walls are highly folded and compose about 10% of the proboscis diameter. The buccal tube is lined with a very low epithelium, which is replaced with a tall one, continuous with that of the buccal cavity, slightly anterior to the buccal cavity.

Buccal mass and oesophagus

The buccal mass is large, slightly less that half of the proboscis length, and lies within the proboscis. It has rather thick walls with no curvature. The buccal lips are very small and poorly defined. Anterior to them, the walls of the buccal tube form a fold, similar in appearance to the true buccal lips. The oesophagus is elongated between the buccal mass and nerve ring and forms a medium-long loop. A buccal sac is absent. The salivary ducts open in the buccal cavity on both sides of the very broad opening of the radular diverticulum.

Glands
The salivary glands are large, paired and acinous. The venom gland changes in histology after passing anteriorly through the nerve ring. The duct is very narrow, ciliated, coiled, and opens at the border between the buccal mass and oesophagus. The muscular bulb is large, with the wall formed of two equal layers of longitudinal muscle fibres, divided by a connective tissue layer, with an innermost, thin layer of circular muscle.

Odontophore and radula
The odontophore is rather large and protrudes into the buccal cavity. It has paired, unfused cartilages, formed by single layer of cells. The radula (Fig. 14c) consists of marginal teeth of the wishbone type, each tooth with a large major limb with a pointed tip, the middle part of the tooth broad and concavo/convex and narrowing towards the base. The secondary limb is thin at the distal end broadening towards the base. The marginal tooth is 172μm in length (1.1% of SL, 4.2% AL)

Haedropleura septangularis (Montagu, 1803)

(Figs 14d, 15)

The specimen sectioned was rather similar to the illustration in Sheridan *et al.* (1973, fig. 6) and differs only in some details.

Rhynchodeum and proboscis
The rhynchodeal sphincter is small and anteriorly located. The epithelium of the anterior half of rhynchodeum wall is tall, glandular and folded. Posteriorly, it is replaced abruptly with a low, non-glandular, cubic epithelium continuous with that of the proboscis wall.

The whole rhynchocoel is rather short and the thick proboscis, although not long, occupies nearly the entire cavity. The ratio between the proboscis length and its diameter is about 1.3. The proboscis tapers toward the tip, which is slightly invaginated at the mouth opening. The proboscis walls are medium-thick and compose about 16% of the proboscis diameter at its base. The mouth opening is very narrow. The muscles of the proboscis wall are equally developed along the length, and only in the inverted part are they somewhat thinner. The proboscis retractor muscles are very large and occupy the whole inner lumen. A large anterior buccal tube sphincter is present, situated somewhat posterior to the proboscis tip. The distance between the sphincter and the uninverted part of the proboscis tip is equivalent to the length of a single radular tooth. A sac-like enlargement of the distal part of the buccal tube is present, but poorly defined. This is lined with loose, tall, ciliated epithelium, while the remaining part of the tube is lined with extremely low, inconspicuous, epithelial cells. There is no intermediate sphincter. The buccal tube has thin walls.

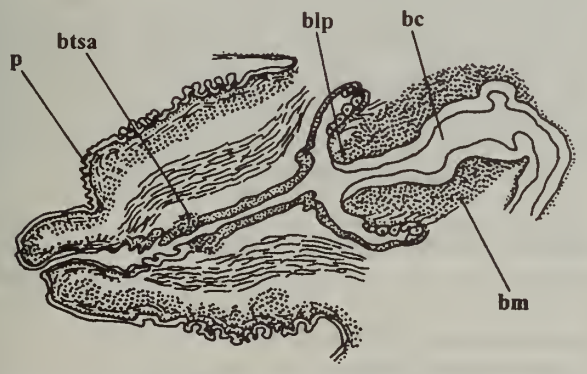

Fig. 15 *Haedropleura septangularis* (Montagu, 1803). Longitudinal section of the proboscis (radular sac not shown).

Buccal mass and oesophagus
The buccal mass lies to the posterior of the proboscis base, and is rather long, equivalent to about two thirds of the proboscis length. It has thick walls and a narrow inner cavity, which is uncurved. Long, extensible, buccal lips are present (not shown by Sheridan *et al.*, 1973). The oesophagus shows no elongation between the buccal mass and nerve ring.

Glands
The salivary glands are paired, large, tubular and coiled. Their diameter is much larger than illustrated by Sheridan *et al.* (1973) and only 2–3 times smaller than that of the venom gland. The salivary ducts are very short, narrower than the glands and ciliated. There is no change in the histology of the venom gland to the anterior of the nerve ring, and it opens into posterior part of the buccal cavity at the boundary with the oesophagus. The venom gland is very large, highly coiled and occupies most of the body haemocoel. The muscular bulb is very large and elongate; longer and thicker in fact than the proboscis. Its wall is formed of two subequal layers of longitudinal muscle fibres, divided by a connective tissue layer, with a very thin innermost layer of circular fibres.

Odontophore and radula
The odontophore is medium-sized, with paired, unfused, odontophoral cartilages. The radula consists of marginal teeth, which are of the wishbone type (Fig. 14d), but with the major element having a large, spathulate, pointed, distal end and a narrow shaft. The minor element is thinner and attaches distally to the broad blade of the major element and to the radula ribbon at the base. The marginal tooth is long, ca.145μm (1.7% of SL, 4.0% AL).

Nquma scalpta Kilburn, 1988

(Figs 16, 17a, 30a)

Rhynchodeum and proboscis
The rhynchodeal sphincter is large and anteriorly situated. The epithelium of the anterior two thirds of the ventral rhynchodeum wall and three quarters of the dorsal wall is tall, glandular, folded and formed of large cells. The epithelium of the posterior rhynchodeum is formed of low, non-glandular, cubic cells continuous with that of the proboscis wall.

The proboscis is long, slightly longer than the rhynchocoel and with the tip not infolded. The proboscis walls are medium-thick, comprising about 13% of the proboscis diameter in its central part. The mouth opening is extremely narrow. The muscles of the proboscis wall are equally developed along its posterior part, but are absent near the distal tip of the proboscis. There is no anterior sphincter of the buccal tube. The distal end of the buccal tube possesses a sac-like enlargement which is lined in the anterior part with very tall and narrow columnar cells where there is also an epithelial pad. The base of a marginal radular tooth was seen attached to the pad. Posterior to the pad, the epithelium is very low, similar to that of the remaining part of the buccal tube, but becomes tall and probably glandular just in front of the large intermediate sphincter, which lies close, about two marginal tooth lengths, distant from the proboscis tip. The buccal tube has rather thin walls.

Buccal mass and oesophagus
The buccal mass is long, equivalent to about 2/3 of the proboscis length and lies at the proboscis base, projecting a long way to the

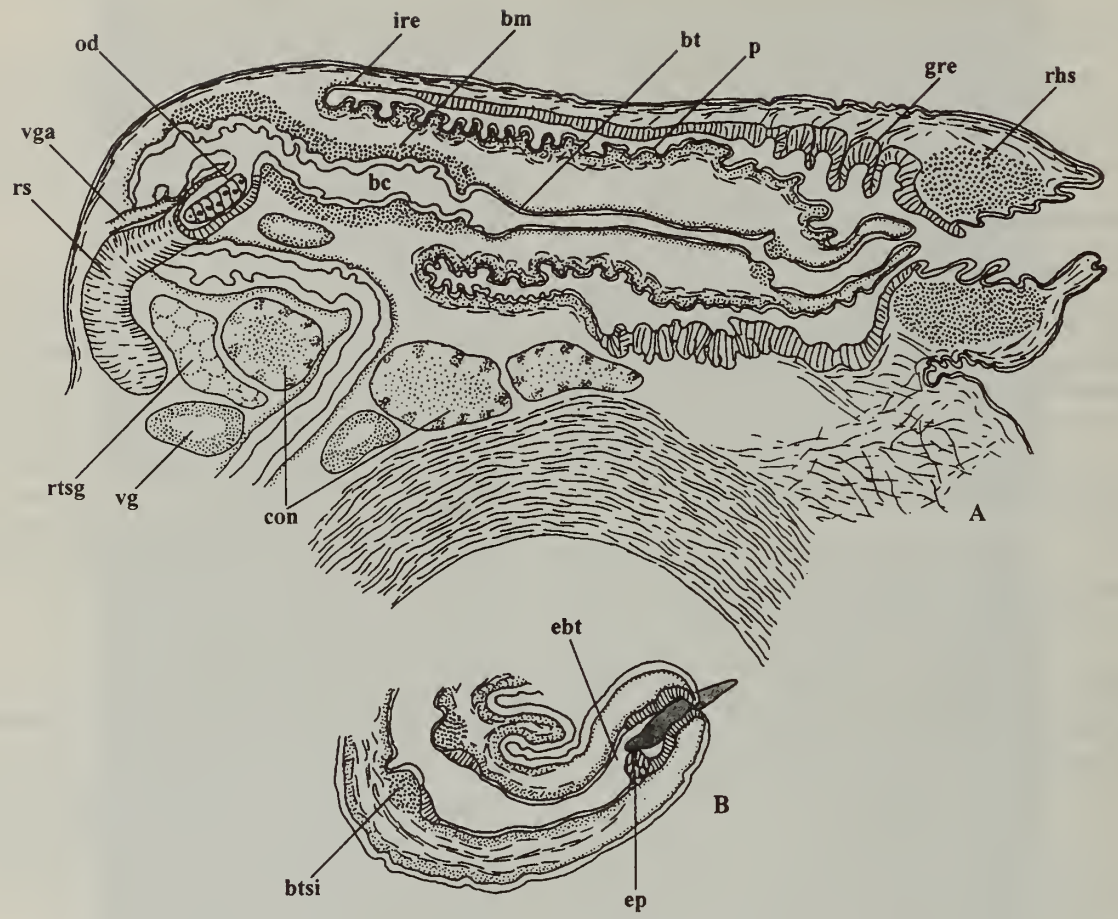

Fig. 16 *Nquma scalpta* Kilburn, 1988. A, Semidiagrammatic longitudinal section of the foregut (salivary ducts not shown); B, longitudinal section of the proboscis tip showing a gripped marginal tooth.

posterior of the rear of the proboscis. It has relatively thin walls and a narrow inner cavity which is uncurved. Extensible buccal lips are absent. The oesophagus is elongated between the buccal mass and nerve ring, forming a rather long loop.

Glands

The salivary glands are large, fused and acinous. The ducts are paired, very long, coiled, thick and leave the gland at the same place. The venom gland changes histology after its anterior passage through the nerve ring. The duct of the gland is narrow, ciliated, long and coiled, and opens into posterior part of the buccal cavity. The wall of the muscular bulb is formed of three layers, the two outermost being divided by a connective tissue layer, with a very thin innermost layer of circular fibres. The two outer layers are formed from longitudinal muscle fibres, the outer being twice as thick as the inner.

Odontophore and radula

The odontophore is small, with paired and unfused, odontophoral cartilages. The buccal sac is short. The radula (Fig. 17a) consist of marginal teeth, with each wishbone tooth formed of two elements. The major element is robust and solid with a distal point. The secondary element is smaller (0.6 of the major element), thinner and terminates before the base of the tooth. The marginal tooth is medium long, ca.130μm (1.3% of SL, 2.7% AL).

Naudedrillia praetermissa (Smith, 1904)

The foregut anatomy is similar in general pattern to that of *Nquma scalpta* and differs in the position of the buccal mass, which lies totally posterior to the proboscis, and the more developed but nevertheless still short buccal lips. The striking difference is that in *N. praetermissa* the salivary glands are tubular, large and highly coiled, with a rather wide inner lumen. The ducts are very short, of similar diameter to the glands, but ciliated.

A radular tooth was seen in the sac-like enlargement of the buccal tube, attached to the epithelial pad. The radula consists of marginal teeth (Kilburn, 1988, fig. 52), with each tooth comprising two components; a large major element which is an elongate, grooved and twisted blade, with a distal point and a shorter minor element which is attached about halfway along the major element. The marginal tooth is long, ca.160μm (1.3% of SL, 3.5% AL).

Epidirona gabensis (Hedley, 1922)

(Fig. 18a)

Rhynchodeum and proboscis

The rhynchostomal sphincter is large and posteriorly located. The rhynchocoel is very long and narrow. The epithelium of nearly the whole rhynchodeal cavity is tall, glandular, folded and formed of

Fig. 17 Radulae of Crassispirinae. a, *Nquma scalpta* scale bar = 20μm b, *Inquisitor latifasciata* scale bar = 25 μm c, *Inquisitor aemula* scale bar = 20 μm d, *Inquisitor* aff. *adenicus* scale bar = 20 μm.

large cells. In approximately the posterior one tenth of the rhynchodeum the epithelium is non-glandular and continuous with that of the proboscis wall.

The proboscis is short in comparison with the rhynchocoel (about 1/5 of its length), rather thick and not coiled. The proboscis walls are thick, forming about 25% of the proboscis diameter. The mouth is very narrow. The muscle of the proboscis walls are equally developed along its length. The anterior buccal tube sphincter is very small and lies posterior to the mouth in front of medium-sized sac-like enlargement of the buccal tube. The epithelium, lining the enlargement forms a large pad, to which the base of a marginal tooth was attached. There is a large intermediate sphincter, situated at about three marginal tooth lengths distant from the mouth opening. The buccal tube has rather thin walls, forming about 10% of the proboscis diameter. It is lined with a tall folded epithelium.

Buccal mass and oesophagus

The buccal mass is large in comparison with the proboscis, equivalent to about two thirds of its length. It lies posterior to the proboscis, with a wide lumen and relatively thin walls. Buccal lips are absent. The oesophagus is greatly elongated between the buccal mass and nerve ring, forming a long loop. Anteriorly, it is wide and flattened, but soon becomes very narrow. There is no buccal sac.

Glands

The salivary glands are large, acinous and fused. The venom gland changes in histology abruptly after passing anteriorly through the nerve ring. The duct is very narrow, unciliated, and opens into the buccal cavity at the posterior border with the oesophagus. The muscular bulb is medium sized, of an irregular oval shape, with its wall consisting of a thick outer layer of circular muscle fibres, a connective tissue layer, a thinner layer of circular fibres and a thin innermost layer of longitudinal fibres.

Odontophore and radula

The odontophore is medium-sized, with the odontophoral cartilages

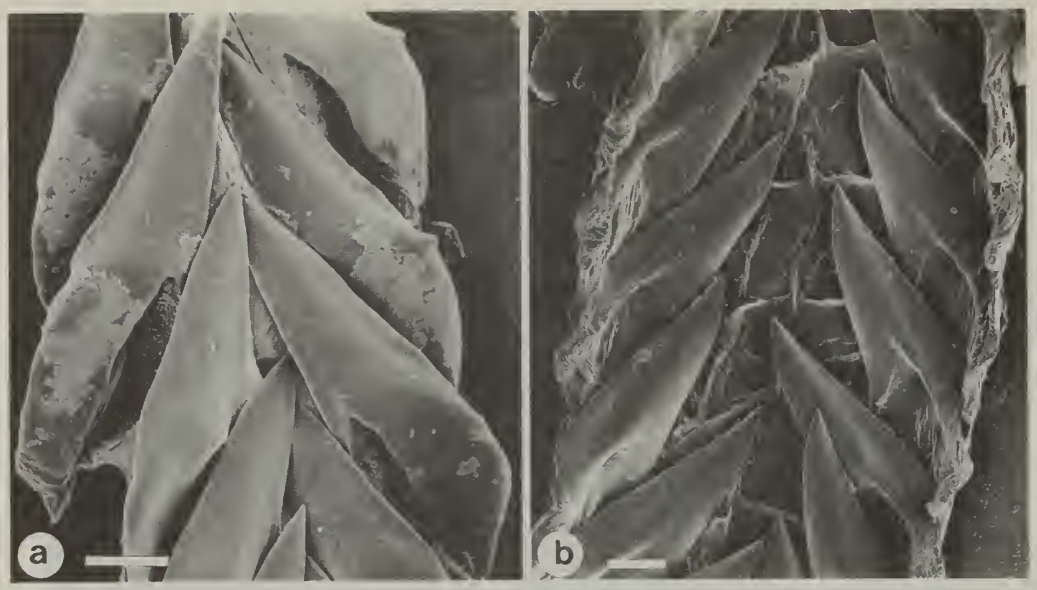

Fig. 18 Radulae of *Epidirona* and *Gemmula* (outgroup). a, *Epidirona gabensis* scale bar = 20μm b, *Gemmula deshayesi* scale bar = 25μm.

paired unfused. The radula is composed of marginal teeth. These teeth (Fig.18a) are of the wishbone type with the distal half tapering to a sharp point, whilst the proximal part of the tooth bifurcates into two more or less equisized limbs. The marginal tooth are medium long, ca.120μm (0.5% of SL, 1.8% AL).

Inquisitor latifasciata (Sowerby, 1870)

(Figs 17b, 20)

See also Taylor (1994, plate 1e,7; figs 11–12)

Rhynchodeum and proboscis

The rhynchodeal sphincter is large and anteriorly situated. The epithelium of the anterior two thirds of the rhynchodeal cavity consists of very tall cells, is glandular, and folded. The epithelium of the posterior one third of the rhynchodeum is continuous with that of the proboscis wall, and consists of low, cubic, non-glandular cells. The rhynchostome is narrow.

The proboscis is long in semi-relaxed animals, and lies coiled within the rhynchodeal cavity. In retracted specimens, the proboscis is very short, less that one third of the rhynchocoel and infolded at the tip. The proboscis wall is not thick in retracted specimens, and comprises about 8% of the proboscis diameter. The mouth is narrow in semi-relaxed animals, but is capable of great stretching and is very wide in retracted specimens (Fig. 20). The muscles of the proboscis wall are equally developed along its length. Both anterior and intermediate buccal tube sphincters are absent and there is no sac-like enlargement of the buccal tube. The buccal tube is very thin-walled in the anterior part (in the inverted position of the proboscis tip), but rather thick posteriorly, where it is nearly equal to the proboscis wall in width. The buccal lips are very large and form the muscular tube, which in retracted specimens extends beyond the mouth of the proboscis.

Buccal mass and oesophagus

The buccal mass is muscular, with thick walls and a rather narrow inner cavity which is not curved. In the retracted state, it lies just within the base of the proboscis, but can clearly be protracted to near the distal tip of the proboscis. There are several retractor muscles, attached to the buccal mass at one end and to the rhynchodeum at the other. The oesophagus is slightly elongated between the buccal mass and nerve ring, forming a short loop.

Glands

The salivary glands are large, paired and acinous. The histology of the venom gland changes abruptly in histology after passing anteriorly through the nerve ring. The duct of the gland is narrow and opens just posterior to the buccal cavity. The muscular bulb wall is formed of two equal layers of longitudinal muscle fibres, divided by a connective tissue layer.

Odontophore and radula

The odontophore is medium sized, with paired, unfused, odontophoral cartilages. The buccal sac is long. The radular comprises marginal teeth only, with each tooth of the wishbone type (Fig. 17b) with a large robust major limb with a distal point and a smaller, slender secondary limb

Inquisitor aemula (Angas, 1877)

(Figs 17c, 21)

Rhynchodeum and proboscis

The rhynchodeal sphincter is medium-sized and anteriorly located. The epithelium of nearly the whole rhynchodeum is glandular and only in a small posterior portion is it low, cubic and non-glandular, like that of the proboscis.

The proboscis is very long, longer than the rhynchodeal cavity and curved when retracted. The proboscis walls are thin, comprising about 10% of the proboscis diameter. The mouth is very narrow, with a low 'rim'. Muscles of the proboscis wall are equally developed along its length. There is no anterior buccal tube sphincter, but there is a large intermediate sphincter, which lies at a distance of about three marginal tooth lengths from the mouth opening. The sac-like enlargement of the buccal tube has a wide lumen, with the epithelium near the mouth opening being columnar and moderately tall, soon becoming low, but forming the epithelial pad, to which a marginal tooth was attached. The buccal tube has moderately thick

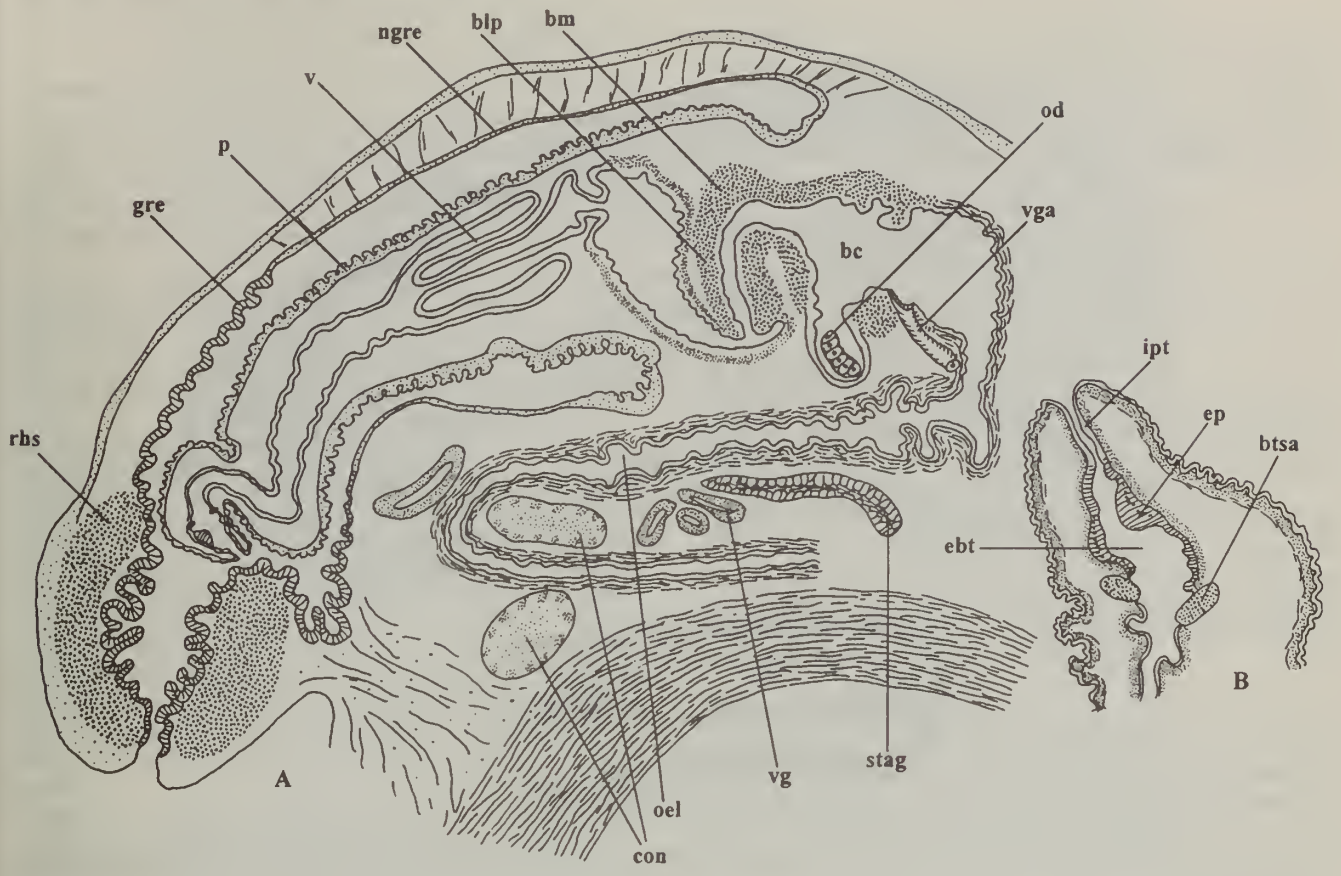

Fig. 19 *Funa jeffreysii* (Smith, 1875). A, Semidiagrammatic longitudinal section of the foregut; B, longitudinal section of the proboscis tip with a gripped marginal tooth.

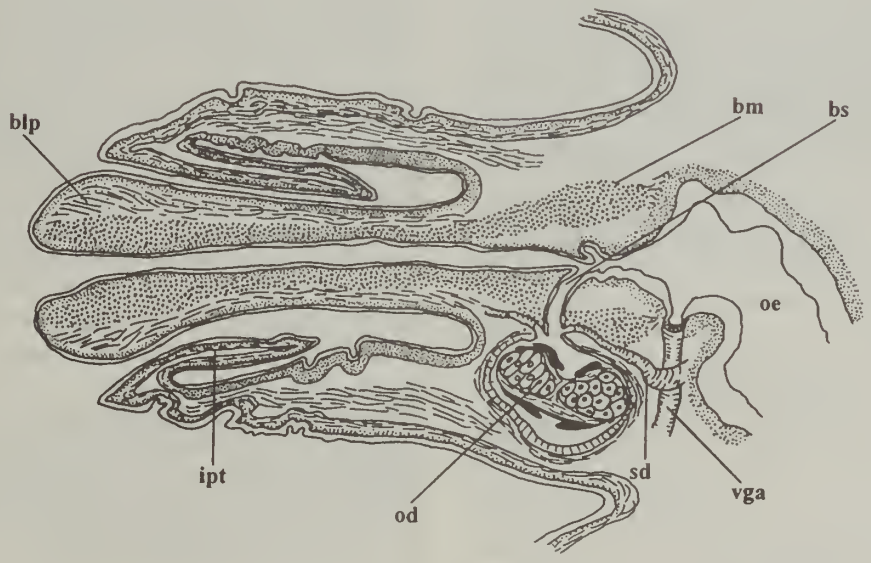

Fig. 20 *Inquisitor latifasciata* (Sowerby, 1870). Longitudinal section of the proboscis and buccal mass in the retracted position.

walls, which are equal in thickness to the proboscis walls. It is wide after the intermediate sphincter, but then greatly reduced in diameter, becoming wider posteriorly (on the drawing the narrowed part of the buccal tube is somewhat shorter, than actual). The buccal lips are small.

Buccal mass and oesophagus

The buccal mass lies within the proboscis and occupies about half the proboscis length. It has rather thin walls and a broad inner cavity, which shows no curvature. The oesophagus is greatly elongated between the buccal mass and nerve ring, forming a long loop.

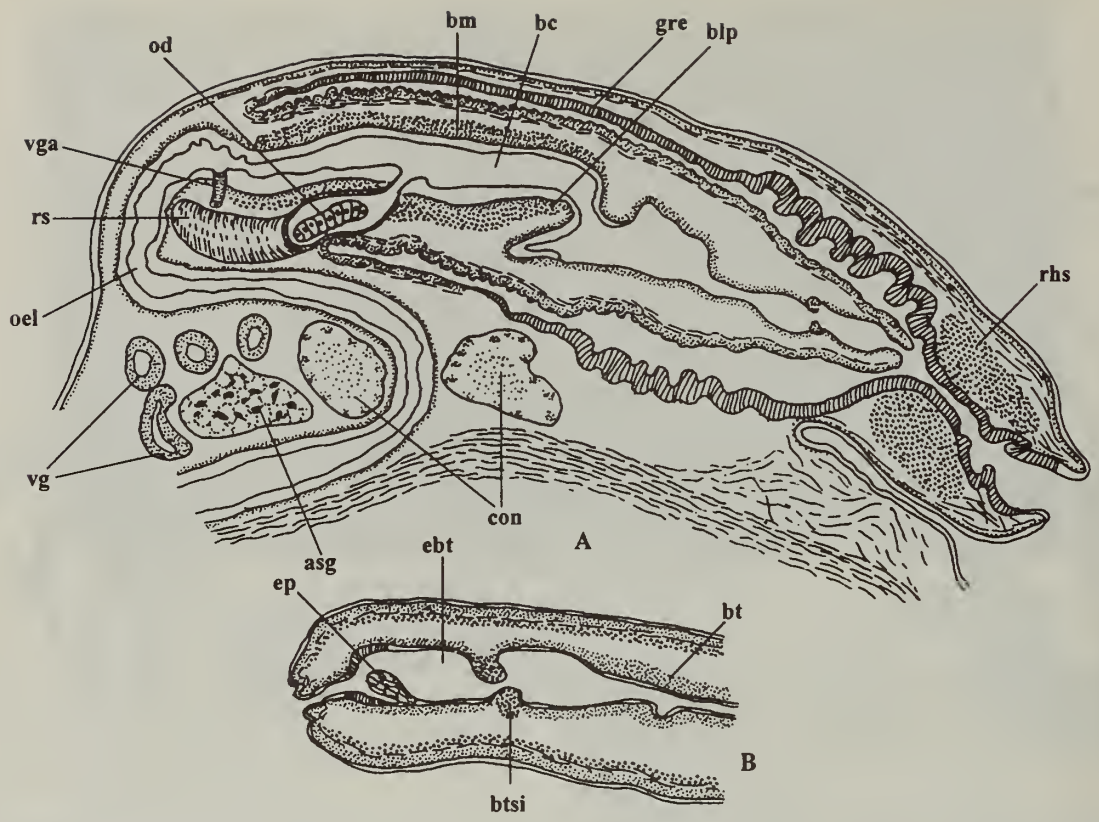

Fig. 21 *Inquisitor aemula* (Angas, 1877). A, semidiagrammatic longitudinal section of the foregut (salivary ducts not shown); B, longitudinal section of the proboscis tip.

Glands
The salivary glands are medium-sized, paired and acinous, with the ducts thick and coiled. The venom gland changes abruptly in histology after passing anteriorly through the nerve ring. The duct of the gland is unciliated, narrow, with thick muscular walls, and opens just posterior to the buccal cavity. The muscular bulb is formed of an outer layer of longitudinal muscle fibres, a connective tissue layer, an inner layer of longitudinal fibres, which is ca. 2.5 times thinner than the outer and finally, a thin, innermost layer of circular muscle fibres. The epithelium lining the inner cavity is rather well developed and non-glandular.

Odontophore and radula
The odontophore is medium-sized, with the odontophoral cartilages paired and unfused. The buccal sac is medium long and very narrow. The radula (Fig. 17c) consists of marginal teeth of the wishbone type, with a robust, solid, pointed, major limb and a smaller thinner, minor limb. The marginal tooth is medium long, ca.130μm (0.6% of SL, 2.3% AL).

Inquisitor aff. *adenicus* Sysoev,1996

(Fig. 17d)

Rhynchodeum and proboscis
The rhynchodeal sphincter is medium large and anteriorly located. The epithelium of nearly whole the rhynchodeum is glandular and for only about one quarter of the posterior portion is it continuous with that of the proboscis wall.

The proboscis is long, and occupies the entire rhynchocoel in one specimen and about half of it in the other. The proboscis walls are thick, and compose about 25% of proboscis diameter. The mouth is very narrow and lined with probable sensory epithelium. The muscles of the proboscis wall are equally developed along its length. The anterior buccal tube sphincter is very small and hardly visible, but the intermediate buccal tube sphincter is large, and lies at a distance of more than two marginal tooth lengths behind the mouth opening. The sac-like enlargement of the buccal tube is well developed, and lined with tall epithelium, which in one specimen forms a pad with a marginal tooth attached to it. The buccal tube has thin walls, about 3–4% of proboscis diameter, lined with a tall epithelium. The buccal lips are very small.

Buccal mass and odontophore
The buccal mass is short, about one third of proboscis length and lies posterior to the base of the proboscis. It is uncurved, with rather thin walls and a broad inner cavity. Several folds of the walls project into the buccal cavity. The buccal mass lies posterior to the proboscis base. The oesophagus is greatly elongated between the buccal mass and nerve ring, forming a long loop.

Glands
The salivary glands are acinous, with thick, uncoiled ducts. The venom gland changes abruptly in histology after passing through the nerve ring. The duct of the gland is narrow and unciliated, with thick muscular walls, and opens just posterior to the buccal cavity. The muscular bulb is large and long, with its wall formed of two nearly equal layers of circular muscle fibres, divided by a connective tissue

layer. The epithelium, lining the inner cavity is rather well-developed in one specimen, but non-glandular.

Odontophore and radula
The odontophore is medium-sized with paired, unfused odontophoral cartilages. A buccal sac is absent. The radula (Fig. 17d) consists of marginal teeth which are of the wishbone type with a robust major limb and a smaller secondary limb. The marginal tooth is short, ca.140μm (0.5% of SL, 1.4% AL).

Funa jeffreysii (Smith, 1875)

(Figs 19, 23d)

See also Taylor (1994, plates 1f, 6a; figs 8 & 9)

Rhynchodeum and proboscis
The rhynchodeal sphincter is large and anteriorly located. The epithelium of the anterior one third of the rhynchodeum is highly folded and glandular, formed of large cells. In the posterior of the rhynchodeum there is an abrupt change to a very low and inconspicuous, non-glandular epithelium which is continuous with that of the proboscis wall.

The proboscis is long, as long as the rhynchodeum, with the tip not infolded. The proboscis walls are thin, comprising about 7% of proboscis diameter. The walls of the buccal tube are similarly thin, composing about 5% of total diameter. The mouth is narrow. The muscles of the proboscis walls are equally developed along its length.

There is a medium-sized, anterior buccal tube sphincter, positioned at the base of the sac-like enlargement of the buccal tube. An epithelial pad is present within the sac-like enlargement. There is no intermediate buccal tube sphincter. The buccal tube is lined with a very low epithelium. It expands greatly to form a long circular fold, which appears like poorly-muscularized, anteriorly-directed lips, similar to the 'valvule' (Sheridan *et al.*, 1973) The buccal lips are large and muscular.

Buccal mass and oesophagus
The buccal mass is large and situated partially within the proboscis base. Its walls are moderately thick. The oesophagus is greatly elongated between the buccal mass and nerve ring, forming a long loop. The walls of the oesophageal loop are thick and formed from distinct longitudinal muscle fibres. The buccal sac is not defined.

Glands
The salivary glands are large, consisting of single tubes, surrounded by acinous cells (acinous tubular type). The ducts are thick and coiled. The venom gland changes in histology while passing anteriorly through the nerve ring. The duct of the gland is narrow, unciliated and opens into the posterior buccal cavity. The muscular bulb is medium-sized, its wall formed of two layers of circular muscle fibres (the outer layer being nearly three times thicker than the middle, divided by a connective tissue layer, with a third innermost, thin layer of longitudinal muscle fibres.

Odontophore and radula
The odontophore is medium-sized, with paired, unfused cartilages. The radula consists of marginal teeth (Fig. 23d which are paddle-shaped with a broad distal blade and a long narrow shaft. The distal tip is pointed, with knife-like edges on either side and a blunt barb. An inconspicuous, thin, secondary limb lies along the margin of the main shaft of the tooth.

Remarks
The unusual feature of this species is that the buccal mass can be protracted way beyond the proboscis tip and out through the rhynchostome (Taylor, 1994, fig. 8). Nevertheless, in the retracted position the buccal mass lies at the proboscis base. It is possible that the presence of the valvule is also connected with the possibility of buccal mass eversion.

Funa latisinuata (Smith, 1877)

(Fig. 23c)

See also Taylor (1994, plate 1g, 6b; fig.10)

Rhynchodeum and proboscis
The rhynchodeal sphincter is large. The epithelium of the anterior one third of the rhynchodeum is highly folded and glandular whilst the posterior is composed of a low, inconspicuous, non-glandular and continuous with that of the proboscis wall.

The proboscis is long, nearly as long as the rhynchodeum and broad with the tip not infolded. The proboscis and buccal tube walls are thin. The mouth is relatively wide. The muscles of the proboscis wall are equally developed along its length. There is a small anterior buccal tube sphincter, but no sac-like enlargement, no epithelial pad and no intermediate sphincter.

Buccal mass and oesophagus
The buccal mass is large and situated partially within the proboscis base and uncurved. Its walls are moderately thick and muscular. The oesophagus is greatly elongated between the buccal mass and nerve ring forming a long loop. The walls of the oesophageal loop are thick and muscular. There is no buccal sac.

Glands
The salivary glands are large and acinous, but with a modified histology. The ducts are thick and coiled. The venom gland changes in histology while passing anteriorly through the nerve ring. The anterior part has thick muscular walls and opens into the posterior part of the buccal cavity. The muscular bulb is medium-sized, with the wall formed from two equisize layers of circular muscles, divided by a thick connective tissue layer, with a very thin innermost layer of longitudinal muscle fibres.

Odontophore and radula
The odontophore is medium-sized, with paired, unfused cartilages. The radula consists of marginal teeth only (Fig. 23c) which are paddle-shaped, with a flattened, angular, barb-less, distal termination, and a long thin shaft. A thin accessory limb lies along the shaft.

Ptychobela suturalis (Gray, 1838)

(Figs 22, 23a, 30c)

Rhynchodeum and proboscis
The rhynchodeal sphincter is medium-sized and situated rather to the posterior of the rhynchostome. The epithelium of the anterior one third of the rhynchodeal cavity is folded and formed of tall, glandular cells. The low, non-glandular epithelium of the posterior two thirds of the rhynchodeum is continuous with that of the proboscis wall. This indicates that a large part of the rhynchodeal wall takes part in proboscis protraction.

In retracted animals, the proboscis is short with the tip infolded (Taylor 1994, fig. 18). However, in relaxed animals, the proboscis is very long, longer that the rhynchocoel and with the tip not inverted.

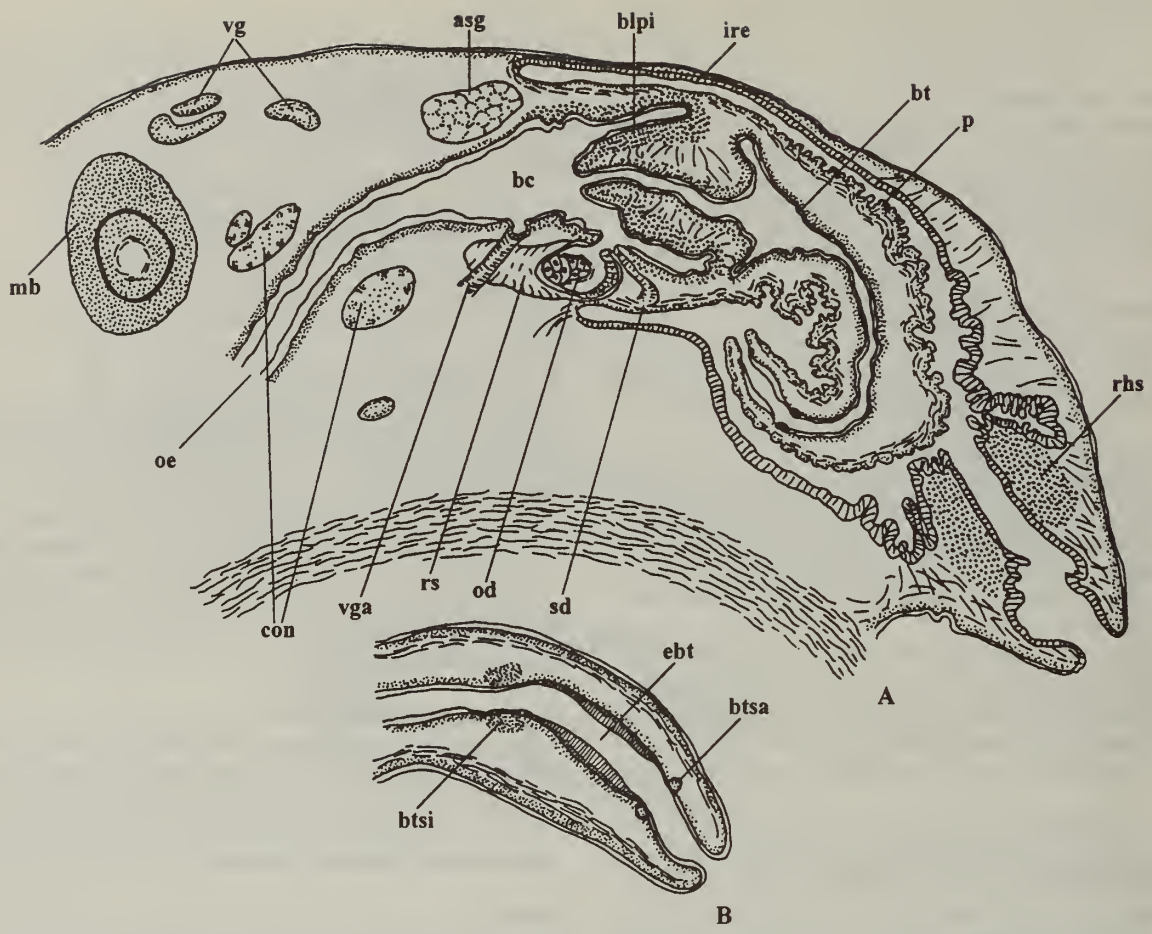

Fig. 22 *Ptychobela suturalis* (Gray, 1838). A, semidiagrammatic longitudinal section of the foregut (only one salivary duct shown) with the proboscis in an everted position and buccal lips inverted inside the buccal cavity; B, longitudinal section of the proboscis tip.

The proboscis walls are medium-thick, and comprise about 15% of the proboscis diameter. The mouth is narrow in relaxed animals, but capable of great expansion. The muscles of the proboscis walls are equally developed along its length.

The buccal tube has a very small anterior sphincter and there is no sac-like enlargement at the distal end There is large intermediate sphincter, which lies about two radular tooth lengths behind the proboscis tip. The buccal tube has rather thick walls, only slightly thinner than those of the proboscis. In the anterior half of the proboscis, the buccal tube is narrow, but greatly expanded posteriorly. There are large, extensible buccal lips which can invert into the buccal cavity. In retracted specimens, they form a muscular tube with a flaring aperture, which extends beyond the mouth of the proboscis.

Buccal mass and oesophagus

The buccal mass lies within the base of the proboscis, and is rather long, comprising about a quarter of the proboscis length, with relatively thin walls and a very broad inner cavity, which is not curved. The oesophagus is elongated between the buccal mass and nerve ring, forming the short loop.

Glands

The salivary glands are large, paired and acinous. The venom gland changes in histology after passing anteriorly through the nerve ring. The duct of the gland is narrow, ciliated, and opens into posterior part of the buccal cavity. The muscular bulb is long, with the wall formed of two equally thick layers of longitudinal muscle fibres, divided by a connective tissue layer and very thin innermost layer of circular fibres.

Odontophore and radula

The odontophore is small with the odontophoral cartilages, paired, and unfused. The buccal sac is very short. The radular teeth (Fig. 23a) are hollow and awl-shaped with a sharp point and broadening towards the base. They are composed of two separate pieces which are fused along one edge and loosely twisted together.

Cheungbeia mindanensis (Smith, 1877)

(Figs 24, 26d, 30d)

See also Taylor (1994, plates 1h, 6d; figs 13–15)

Rhynchodeum and proboscis

The rhynchodeal sphincter is large and anteriorly located and the rhynchostome is relatively wide. The epithelium of the anterior half of the dorsal wall of the rhynchodeal cavity is glandular (dorsal wall is significantly longer than the ventral). In the posterior part of the rhynchodeum the epithelium is non-glandular and continuous with that of the proboscis wall. The proboscis is extremely long and lies coiled within the rhynchocoel. The proboscis walls are highly folded and comprise about 15% of the proboscis diameter. The muscles of

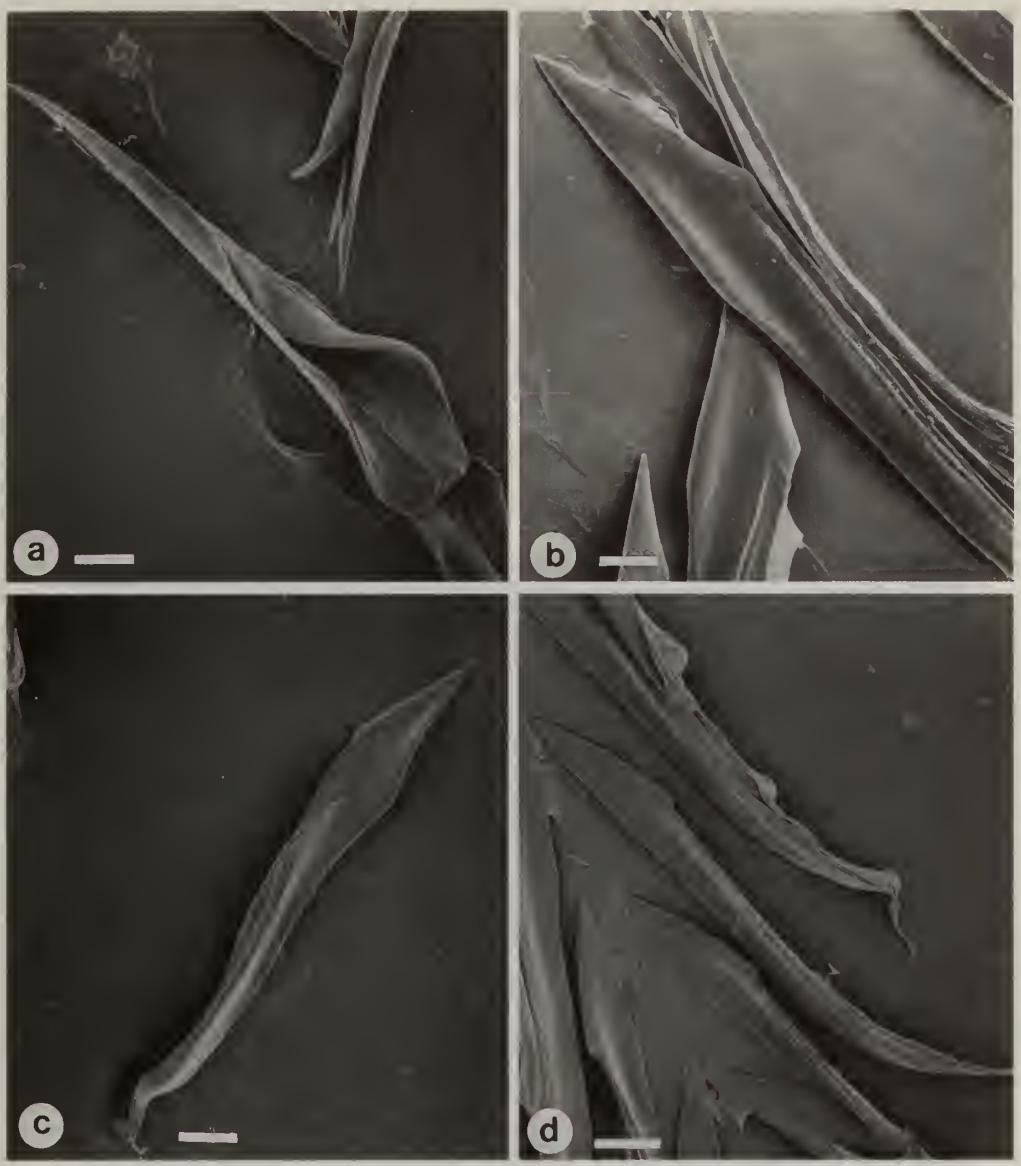

Fig. 23 Radulae of Crassispirinae. a, *Ptychobela suturalis* scale bar = 20μm b, *Vexitomina garrardi* scale bar = 20μm c, *Funa latisinuata* scale bar = 50μm d, *Funa jeffreysii* scale bar = 60μm.

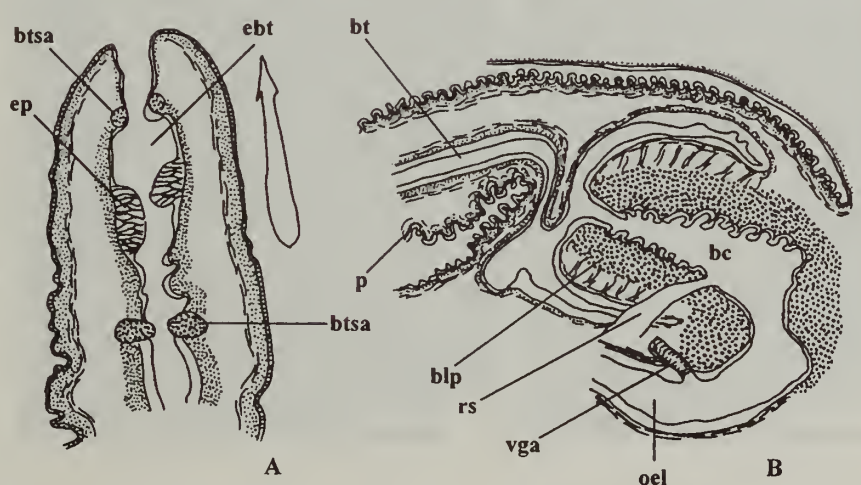

Fig. 24 *Cheungbeia mindanensis* (Smith, 1877) A, longitudinal section of the proboscis tip, the tooth at the same scale shown below; B, longitudinal section of the proboscis base and buccal mass (salivary ducts not shown).

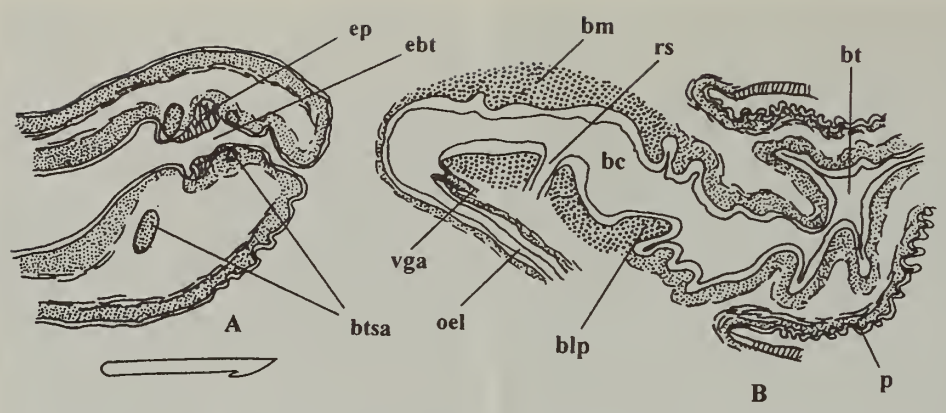

Fig. 25 *Cheungbeia robusta* (Hinds, 1843). A, longitudinal section of the proboscis tip, with a tooth shown at the same scale below; B, longitudinal section of the proboscis base and buccal mass.

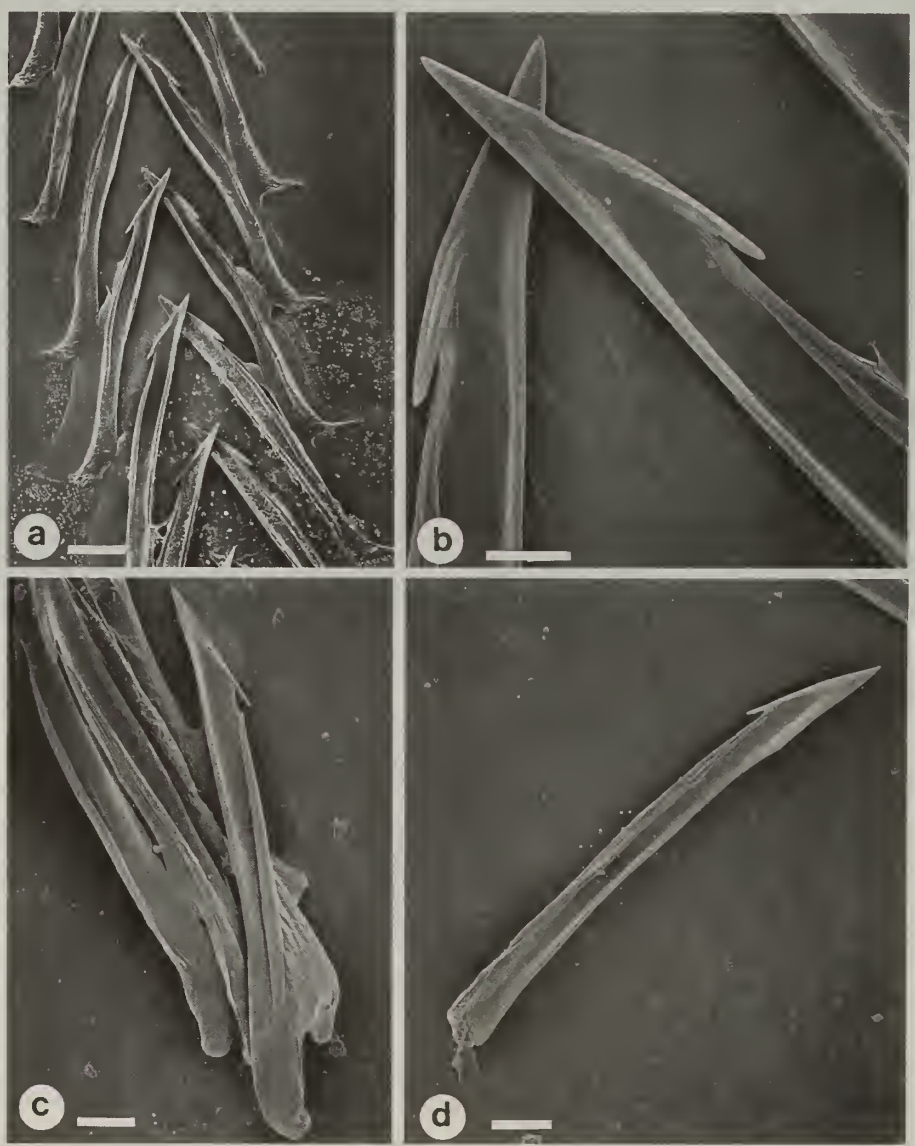

Fig. 26 Radulae of *Cheungbeia*. a–c, *Cheungbeia robusta*, a, portion of radula with two rows of teeth, scale bar = 30μm b, detail of tooth tip scale bar = 10μm c, single tooth, note secondary limb (arrowed) along edge of major limb scale bar = 20μm d, *Cheungbeia mindanensis* single tooth with secondary limb arrowed. scale bar = 25μm.

the proboscis wall are equally developed along its length. The mouth is narrow. The proboscis is covered with ciliated epithelium with long cilia, which is replaced by non-ciliated epithelium with a rather thick cuticle at its base.

A small, anterior, buccal tube sphincter lies in front of the sac-like enlargement of the buccal tube, close to mouth opening. The epithelium, lining the enlargement is tall, forming pads on both walls (Fig. 30d). A second larger sphincter lies at the base of the enlargement at the distance slightly longer than one tooth length and therefore should be considered as anterior. The walls of the buccal tube are thin in the anterior part, but become rather thick (about 10% of proboscis diameter) after the second sphincter.

Buccal mass and oesophagus
The buccal mass lies at the proboscis base and is short in comparison to the proboscis. It is thick-walled, with a broad lumen and curved. There are very large, extensible buccal lips. The oesophagus is greatly elongated between buccal mass and nerve ring and forms a long loop. There is no buccal sac. The opening of the radular diverticulum is narrow and relatively long. The salivary ducts open into the buccal cavity on both sides of the opening of the radular diverticulum.

Glands
The salivary glands are medium-sized, paired and acinous. The venom gland changes markedly in histology after passing through the nerve ring. The duct is very narrow, unciliated and opens at the border between the buccal mass and oesophagus. The muscular bulb is medium-sized, with the wall formed from two layers of longitudinal muscle fibres (the outer about twice as thick as the inner), divided by a connective tissue layer, with a thin, innermost layer of circular muscle.

Odontophore and radula
The odontophore is rather large, with paired, unfused cartilages. The radula consist of marginal teeth (Fig. 26d), which are long and harpoon-like in form, but concavo-convex (gutter-shaped) in profile. The distal end of the tooth is sharply pointed with a pronounced barb, whilst the shaft is more or less straight-sided, with just a slight enlargement at the base. A very thin secondary limb lies along the edge of the shaft (Fig. 26d). The marginal tooth is very long, ca. 320μm (1.3% of SL, 4.0% AL).

Cheungbeia robusta (Hinds, 1843)

(Figs 25, 26a–c)

See also Taylor (1994, plates 1i, 6c; figs 16–17)

Rhynchodeum and proboscis
The rhynchodeal sphincter is large and located slightly to the posterior. The epithelium of nearly the whole wall of the rhynchodeal cavity is glandular, whilst only a small posterior portion is non-glandular and continuous with that of the proboscis wall. The rhynchostome is rather wide.

The proboscis is very long, longer than the rhynchocoel and coiled within it. It is relatively wide at the base and narrows towards the tip. The walls of the proboscis are thin and highly folded, forming about 10% of the proboscis diameter. Muscles of the proboscis wall are equally developed along its length. The mouth is narrow. The anterior, buccal tube sphincter is very small and lies close to the mouth opening, in front of the short, only slightly differentiated, sac-like enlargement of the buccal tube The epithelium lining this enlargement is tall, forming pads on both walls. A second, larger sphincter lies at the base of the enlargement at slightly more than one radular tooth length from the mouth and therefore should be considered as an anterior sphincter. The buccal tube is narrow anteriorly, but expands greatly posterior to the sac-like enlargement and occupies nearly the whole proboscis lumen. Nevertheless, its walls are thin and form only about 5% of the proboscis diameter at its base.

Buccal mass and oesophagus
The buccal mass is long, thick-walled with broad lumen, curved, and lies at the proboscis base. The boundary between the posterior buccal tube and the buccal mass is not well defined. The buccal lips are very short. The oesophagus is greatly elongated between buccal mass and nerve ring and forms a long loop, which is narrow when leaving the buccal cavity and expands posteriorly. There is no buccal sac. The opening of the radular diverticulum is rather narrow and moderately long. The thick and long salivary ducts open in the buccal cavity on both sides of the opening of the radular diverticulum.

Glands
The salivary glands are medium-sized, paired, and of the modified acinous type. The venom gland changes abruptly in histology after passing through the nerve ring. The duct is very narrow, unciliated and opens at the border between the buccal mass and oesophagus. The muscular bulb is large, with the wall mainly formed of two layers of circular muscle fibres (the outer being about twice the thickness of the inner), divided by a connective tissue layer, with a thin, innermost layer of circular muscle.

Odontophore and radula
The odontophore is small, with paired, unfused cartilages. The radula consist of marginal teeth only (Figs 26a–c) which are harpoon-like and very similar to those of *Cheungbeia mindanensis* (Fig. 26d). These have long shafts which are concavo-convex (gutter shaped) in profile. The distal end of the tooth is sharply pointed with a pronounced barb, whilst the shaft is more or less straight-sided, with just a slight enlargement at the base. A very thin secondary limb lies along the edge of the shaft (Fig. 26c).

Antiguraleus morganus (Barnard, 1958)

(Figs 27, 28a)

Rhynchodeum and proboscis
The rhynchodeal sphincter is medium-sized and anteriorly located. The epithelium of the anterior half of the rhynchodeal cavity is tall, glandular, folded and formed of large cells, while that of the posterior half of the rhynchodeum is non-glandular and continuous with that of the proboscis wall. This posterior part of the rhynchodeum is attached by numerous muscle fibres to the body wall and probably cannot be everted. The rhynchostome is narrow.

The proboscis is very long, more than twice as long as the rhynchodeal cavity, rather thin and coiled. The proboscis walls comprise about 15% of the proboscis diameter. The mouth is very narrow. The muscles of the proboscis wall are equally developed along its length. The anterior buccal tube sphincter is small, and lies in front of a very broad sac-like enlargement of the buccal tube. The epithelium, lining the enlargement is similar to that of the rest of the buccal tube. Additionally, there is large intermediate sphincter, situated approximately half-way along the proboscis. The buccal tube has rather thin walls, forming about 8% of proboscis diameter.

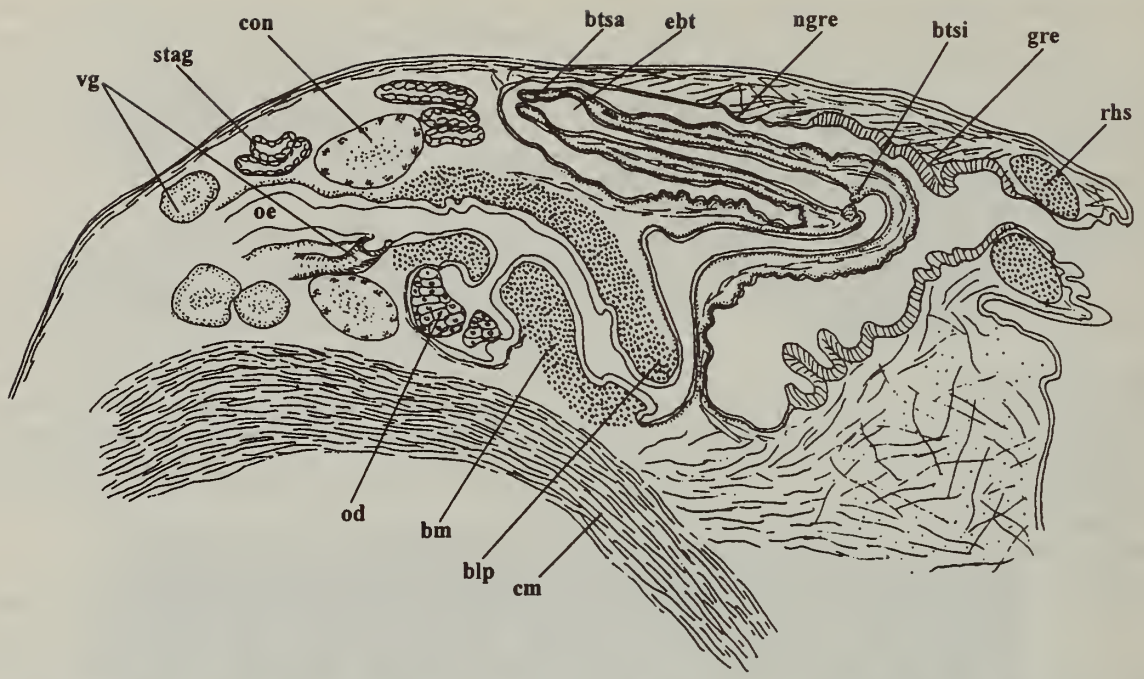

Fig. 27 *Antiguraleus morganus* (Barnard, 1958). Semidiagrammatic longitudinal section of the foregut (salivary glands not to scale).

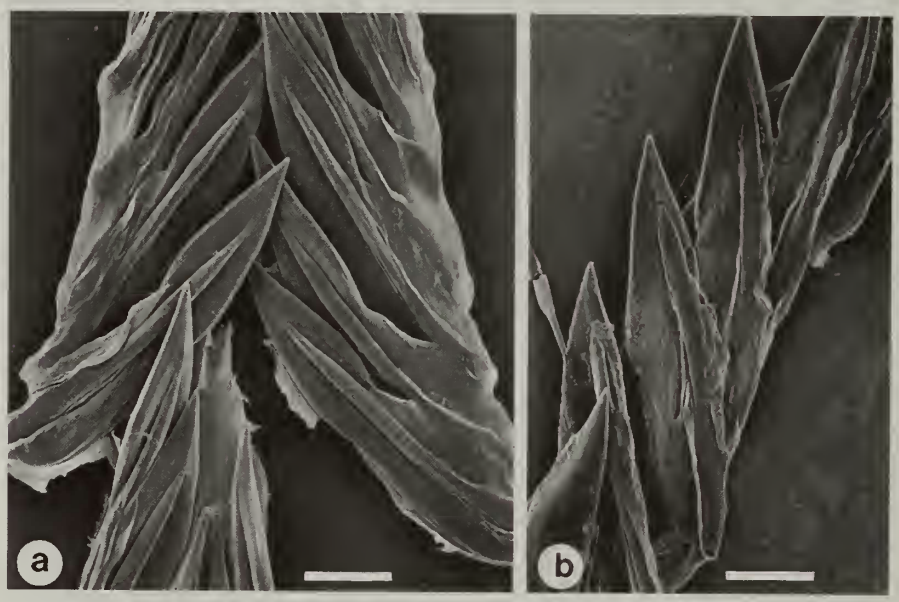

Fig. 28 Radulae of Crassispirinae. a, *Antiguraleus morganus* b, *Paraguraleus costatus*. Scale bars = 20μm.

Buccal mass and oesophagus

The long, buccal mass lies posterior to the proboscis, and is equivalent to nearly half of the proboscis length, with thick walls and a rather broad inner cavity, which is not curved. There are large extensible buccal lips. The oesophagus is not elongated between buccal mass and nerve ring, which is situated closely posterior to the buccal mass. A buccal sac is absent.

Glands

The salivary glands are large, paired, and consist of single, coiled tubes but with the acinous morphology. The venom gland does not change histology after passing anteriorly through the nerve ring. It opens at the border between the buccal mass and oesophagus just in front of the nerve ring. The muscular bulb is small, the wall formed of two equal layers of longitudinal fibres, divided by a connective tissue layer, with an innermost very thin layer of circular muscle.

Odontophore and radula

The odontophore is medium-sized, with a pair of unfused cartilages formed of one layer of cells. The radula consists of marginal teeth of the wishbone type (Fig. 28a). The major limb of the tooth is elongate with a pointed tip and a constricted waist in the middle of the tooth. Below this constriction, the lower marginal edge of the tooth is extended as a 'soft' buttress to attach to the radular membrane. The minor element is slender and shorter, attached to the distal blade of the major element and broadens slightly at the base, where it attaches to the membrane. The marginal teeth are long, ca.120μm (1.2% of SL, 3.2% AL).

Guraleus costatus (Hedley, 1922)

(Fig. 28b)

Unfortunately, the specimen was sectioned nearly transversely and an illustration of it comparable with the other species was not possible.

Rhynchodeum and proboscis

The rhynchodeal sphincter is small and anteriorly located. The epithelium of the anterior part of the rhynchodeal cavity is glandular, whilst that of the posterior rhynchodeum is nonglandular and continuous with that of the proboscis wall. The non-glandular posterior part of the rhynchodeum is very thin and attached by numerous muscle fibres to the body wall and probably cannot be everted. The rhynchostome is narrow.

The proboscis is very long and coiled, more than twice as long as the rhynchodeal cavity. It is very thick at the base but narrows towards the tip (diameter of 0.44 mm at the base, but only 0.08 at the tip), The proboscis walls are thin, comprising less than 7% of the proboscis diameter at its base. The mouth is very narrow. A very small, anterior buccal tube sphincter, lies in front of a small, sac-like enlargement of the buccal tube. The epithelium, lining the enlargement is similar to that of the rest of the buccal tube. A single tooth was seen in the enlargement. There is large intermediate sphincter, situated approximately midway down the proboscis. The buccal tube is very narrow anteriorly, but broad in the posterior part of the proboscis. Its walls are very thin and highly folded.

Buccal mass and oesophagus

The buccal mass lies within the base of the proboscis, with thick walls and rather broad inner cavity, and showing no curvature. There are large, extensible, buccal lips, which can be inverted inside the cavity. The oesophagus is slightly elongated between buccal mass and nerve ring and forms a short loop. There is no buccal sac. The salivary ducts open into the buccal cavity on both sides of the opening of the radular diverticulum.

Glands

The salivary glands are small, paired and acinous. The venom gland changes abruptly in histology after passing through the nerve ring. The duct is very narrow, unciliated and opens at the border between the buccal mass and oesophagus. The muscular bulb is large, the wall is formed of two equal layers of longitudinal fibres, divided by a connective tissue layer, with a thin, innermost layer of circular muscle.

Odontophore and radula

The odontophore is rather large with a pair of unfused cartilages. The radula consists of marginal teeth of the wishbone type (Fig. 28b). Each tooth has a robust and pointed major limb with a straight, blade-like leading edge. The secondary limb is long and slender and attached to the major limb near the distal tip. The marginal teeth are very long, ca.105µm (1.4% of SL, 4.2% AL).

Burchia spectabilis Sysoev & Taylor, 1997

(Fig. 29)

See Sysoev & Taylor (1997, fig. 3)

Rhynchodeum and proboscis

The rhynchodeal sphincter is very large, and located slightly to the posterior. The anterior one third of the rhynchodeal cavity possesses a very tall, glandular, folded epithelium formed of large cells. The epithelium of the posterior two thirds of the rhynchodeum is continuous with that of the proboscis wall and is low, cubic and non-glandular. This indicates, that the greater part of the rhynchodeal lining is involved in proboscis protraction. The rhynchostome is narrow.

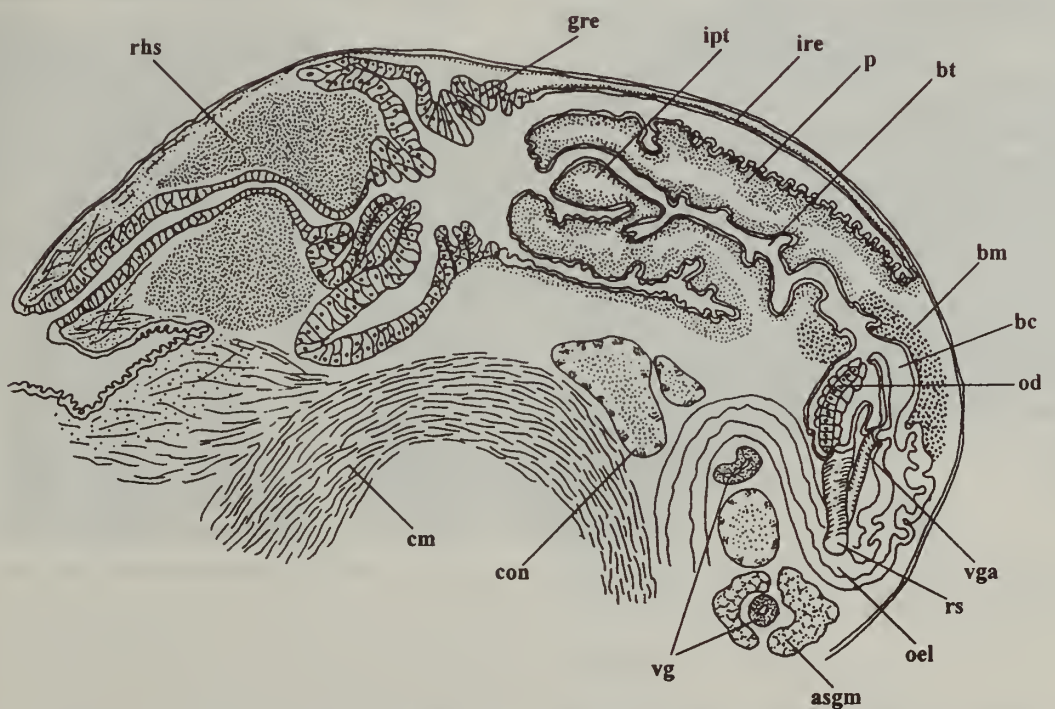

Fig. 29 *Burchia spectabilis* Sysoev & Taylor, 1997. Semidiagrammatic longitudinal section of the foregut (salivary ducts not shown).

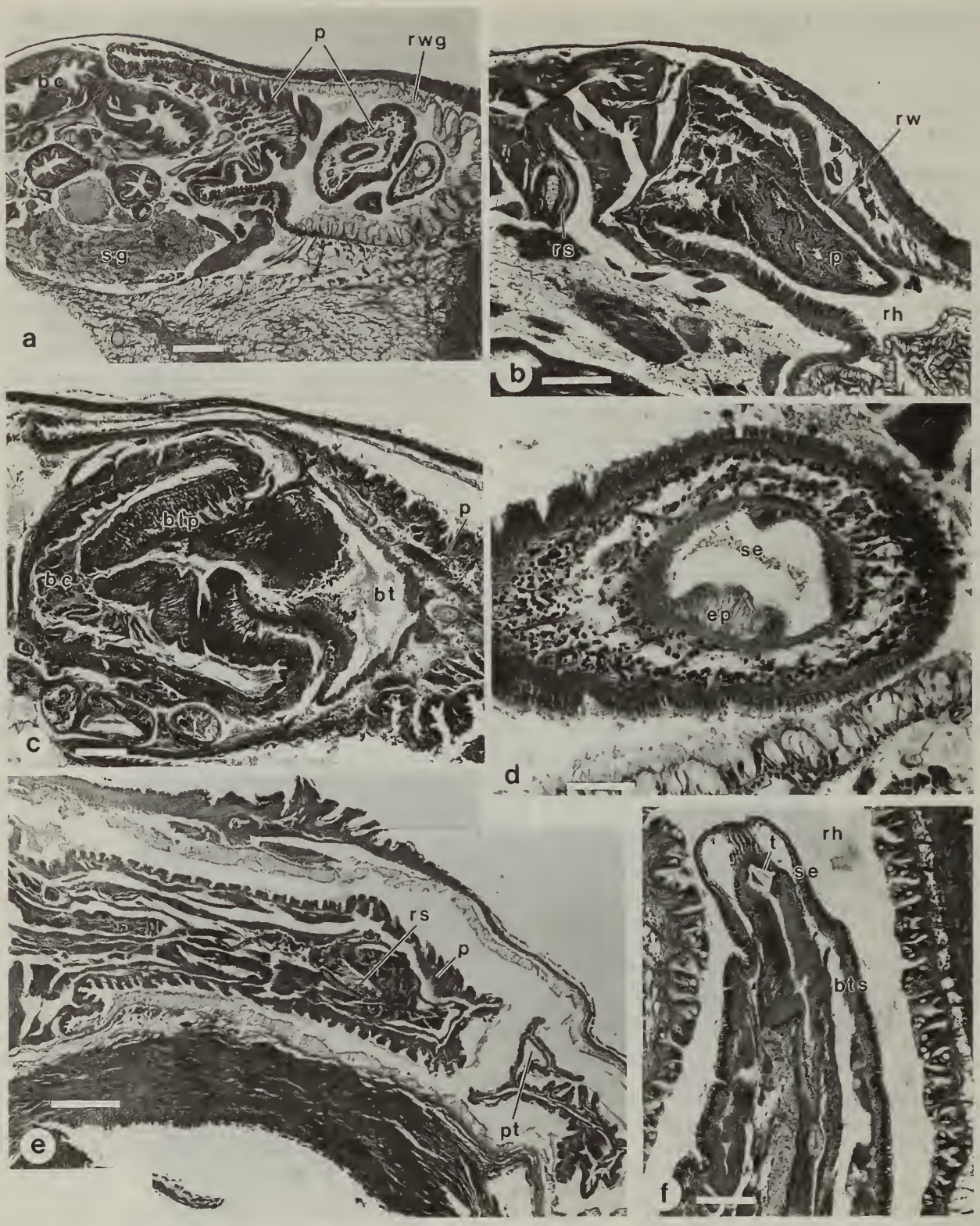

Fig. 30 a, *Nquma scalpta*, longitudinal section of foregut showing proboscis and glandular anterior part rhynchodeal wall. Scale bar = 250μm b, *Vexitomina garrardi* showing proboscis and muscular wall of the posterior rhynchodeum continuous with proboscis wall and also the radular sac located some distance to the posterior of the proboscis base. Scale bar = 250μm c, *Ptychobela suturalis* showing large buccal lips, inverted into the buccal cavity. Scale bar = 250μm d, *Cheungbeia mindanensis*, sac-ike enlargement of the buccal tube near the proboscis tip showing the pad of tall epithelial cells. Scale bar = 60μm e, *Crassispira harfordiana flucki*, long proboscis in the rhynchocoel showing the radular sac located in the anterior part of the proboscis and the complex folding of the proboscis tip (see Fig. 6). Scale bar = 250μm f, longitudinal section of the proboscis tip of the outgroup *Gemmula deshayesi* (Turrinae) showing the wishbone tooth held in the sac-like enlargement of the buccal tube and the intermediate sphincter located several tooth lengths from the proboscis tip. Scale bar = 250μm.

The proboscis is long and thick, and occupies about two thirds of the rhynchodeal cavity. The proboscis walls are thick and comprise about 20% of the total diameter. The mouth is narrow in the preserved condition, but appears capable of great enlargement. The ventral side of the anterior part of the proboscis wall is invaginated. The muscles of the proboscis wall are equally developed along its length. Both anterior and intermediate buccal tube sphincters are absent, as is also the distal sac-like enlargement of the buccal tube.

Buccal mass and oesophagus
The buccal mass is situated to the posterior of the base of the proboscis. It is long, equivalent to about half of the proboscis length, with thick walls and a rather narrow inner cavity, which is not curved. Extensible buccal lips are absent. The oesophagus is elongated between the buccal mass and nerve ring, forming a short loop.

Glands
The salivary glands large and acinous. The venom gland shows a change in histology after passing anteriorly through the nerve ring. The duct of the gland is narrow, ciliated and opens into the posterior part of the buccal cavity. The muscular bulb is long with the wall formed of two layers of equal thickness composed of longitudinal fibres, divided by a connective tissue layer.

Odontophore and radula
The odontophore is medium-sized, with paired, unfused, odontophoral cartilages formed of one layer of cells. The radula comprises marginal teeth, which are of the robust, wishbone form, with a long solid, distally pointed major limb and a thinner secondary limb, which attaches near the tip of the major limb. The marginal teeth are short, ca. 165µm (0.5% of SL, 1.4% AL).

Vexitomina garrardi (Laseron, 1954)

(Figs 23b, 30b)

Rhynchodeum and proboscis
The rhynchodeal sphincter is large, long and situated slightly towards the posterior. The epithelium of the anterior two thirds of the rhynchodeum is glandular, forming tall folds, whilst the epithelium of the posterior one third of the rhynchodeum is non-glandular and continuous with that of the proboscis wall. The rhynchostome is wide. The proboscis is short, cone-shaped, and occupies about half the rhynchocoel. The proboscis walls form about 20% of the proboscis diameter. The muscles of the proboscis walls are equally developed along its length. The mouth is very narrow.

The anterior buccal tube sphincter is small, and lies close to the mouth, opening in front of the long sac-like enlargement of the buccal tube. A tall epithelium lines the enlargement. A second, larger sphincter lies at the base of the enlargement, at a distance slightly longer than one tooth length and therefore should be considered as anterior. A tooth was seen in the buccal tube posterior to the latter sphincter. The buccal tube walls are rather thin (about 8% of proboscis diameter) and highly folded. In the posteriormost part the tube forms a very long, but narrow, circular fold.

Buccal mass and oesophagus
The buccal mass is large in comparison with the proboscis, equivalent to about two thirds of its length, with thick, folded walls and a narrow lumen. It lies posterior to the proboscis base. The buccal lips are small. The oesophagus is elongated between the buccal mass and nerve ring and forms a short loop. After leaving the buccal cavity, the oesophagus is very narrow, but then expands greatly after passage through the nerve ring. The buccal sac is very short.

Glands
The salivary glands are medium-sized, paired, and acinous. The venom gland changes sharply in histology after passing anteriorly through the nerve ring. The duct is very narrow, unciliated and opens at the border between the buccal mass and oesophagus.

The muscular bulb is medium-sized, with the wall formed of two layers of longitudinal muscle fibres (the outer being twice as thick as the inner), divided by a connective tissue layer and innermost thin layer of circular muscle.

Odontophore and radula
The odontophore is medium-sized, with paired, unfused cartilages. The radula consists of marginal teeth (Fig. 23b) which are long, with a blade-like distal portion, which is sharply pointed with a small barb. The shaft is long and tapers gradually towards the base. The teeth are slightly concavo-convex in profile and a very thin splint-like secondary limb lies along the edge of the shaft.

Turridrupa bijubata (Reeve, 1843)

Rhynchodeum and proboscis
The rhynchodeal sphincter is medium-sized and posteriorly located. The anterior half of the rhynchodeum has a highly folded, tall, glandular epithelium whilst the posterior half has a low cubic epithelium similar to that of the proboscis wall. The proboscis is short and occupies about half of the rhynchodeum, the tip is thin, while the base is thicker and muscular. There is a very small anterior buccal tube sphincter, lying at the distal end of a small sac-like enlargement containing a single radular tooth. A larger intermediate sphincter lies at a distance of about 10 tooth lengths from the proboscis tip.

Buccal mass and oesophagus
The buccal mass is long and curved and lies to the posterior of the proboscis. The walls of the buccal mass are long and muscular anterior to the entrance of the radular sac and the buccal lips small and not invertible. The oesophagus is not elongated between the buccal sac and nerve ring.

Glands
The salivary glands are large, paired and acinous, with large ciliated ducts. The venom gland changes abruptly in histology after passing anteriorly through the nerve ring and the duct opens into the oesophagus just posterior to the buccal mass. The muscular bulb is large and comprises two layers of circular muscle separated by a connective tissue layer. The outer layer is about twice as thick as the inner. There is no thin, innermost, muscular layer.

Odontophore and radula
The odontophore is large with two large unfused cartilages. The radula consist of both central and marginal teeth (Kilburn, 1988, fig. 40). The central tooth comprises a square plate with a prominent spine-like cusp. The marginal teeth are of the robust wishbone type with the bifurcating proximal end, similar to *Epidirona gabensis* (Fig. 18a).

Outgroup

This species from the family Turrinae, was chosen as the outgroup. The anatomy and radula is described and illustrated in Taylor (1994) and further details are given below.

Gemmula deshayesii (Doumet, 1839)

(Figs 18b, 30f)

Rhynchodeum and proboscis

There is a large rhynchodeal sphincter situated slightly to the posterior. The rhynchodeum has a folded epithelium of tall glandular cells for its entire length.

The proboscis is long, nearly as long as the rhynchodeum. The proboscis walls are medium thick about 15% of total diameter, whilst the walls of the buccal tube are thin forming about 5% of the diameter. The muscles of the proboscis wall are less developed near the tip. There is a small anterior buccal tube sphincter, with a short sac-like enlargement and epithelial pad. A single wishbone radular tooth was held in the enlargement. An large intermediate buccal tube sphincter lies at about five tooth lengths from the mouth.

Buccal mass and oesophagus

The buccal mass is short, muscular and uncurved and lies within the base of the proboscis. The buccal lips are medium long and invertible. The oesophagus is not elongated between the nerve ring and buccal mass.

Glands

Salivary glands are large and acinous with paired ducts. There is no change in the histology of the venom gland to the anterior of the nerve ring. The gland opens into the rear of the buccal cavity by a short ciliated duct. The muscular bulb comprises two subequal layers of circular muscle divided by a connective tissue layer.

Odontophore and radula

There a two medium-sized odontophoral cartilages. The buccal sac is medium long. The radula consist of both central and marginal teeth (Fig. 18b) The central tooth is wide and low with a central spine-like cusp. The marginal teeth are wishbone in form, but of the 'clothes-peg' type with pointed tips and bifurcated proximal ends.

CHARACTER ANALYSIS AND RELATIONSHIPS WITHIN THE CRASSISPIRINAE

Characters and states

On the basis of the analysis of the thin sections described above and previous work (Taylor *et al.*, 1993) we selected 20 characters with potential for determining relationships between the species studied. These characters and their states are listed in Table 2. Many of these are self explanatory or reference is given to figures which illustrate the various states. However, further explanation of some characters is given below.

Character 2. In some species, such as *Inquisitor latifasciata* and *Ptychobela suturalis*, the proboscis tip may be inverted deeply into the buccal tube (Fig. 20).

Character 5. In some species there is an epithelial pad of large cubic cells in the anterior part of the buccal tube (*C. (Gibbaspira) dysoni*, Fig. 5).

Character 7. In many species there is a sac-like enlargement of the anterior part of the buccal tube. This is often lined with an epithelium of tall cells. The function of the sac is to hold single detached radular teeth at the proboscis tip (Fig. 30d).

Character 9. Some taxa possess large buccal lips which are often capable of inversion into the buccal cavity; in others this was not observed.

Character 11. In many species there is a sharp bend within the buccal mass (e.g. Fig. 9), while other species show no curvature.

Table 2 List of characters and states used in the cladistic analysis

1. Epithelium of posterior rhynchodeal wall: 0 – glandular; 1 – continuous with proboscis wall for less than ½ of the rhynchodeum length; 2 – continuous with proboscis wall for more than ½ of the rhynchodeum length.
2. Proboscis tip: 0 – not inverted inside; 1 – inverted inside.
3. Proboscis tip epithelium: 0 – not invaginated; 1 – invaginated.
4. Proboscis length: 0 – very long (longer than rhynchodeum); 1 – long (50–100% of rhynchodeum length); 2 – short (less than 50% of rhynchodeum length).
5. Epithelial pad at tip of buccal tube: 0 – present; 1 – absent.
6. Anterior buccal tube sphincters (the distance from the sphincter to the mouth opening is less than the radular tooth length): 0 – one; 1 – two; 2 – absent.
7. Sac-like enlargement of the buccal tube with tall epithelium: 0 – present; 1 – absent.
8. Intermediate sphincter of the buccal tube (the distance from the sphincter to the mouth opening is more than the tooth length): 0 – absent; 1 – present.
9. Buccal lips: 0 – large invertible; 1 – large uninvertible; 2 – small; 3 – absent.
10. Position of the buccal mass: 0 – posterior to the proboscis base; 1 – at the proboscis base; 1 – within the proboscis (up to near tip).
11. Buccal mass shape: 0 – not curved; 1 – curved.
12. Elongation of the oesophagus between buccal mass and nerve ring: 0 – absent; 1 – present.
13. Salivary glands: 0 – acinous; 1 – modified acinous; 2 – acinous tubular; 3 – simple tubular; 4 – anastomosing tubular.
14. Histology of the venom gland anterior to the nerve ring: 0 – unchanged; 1 – changed.
15. Position of opening of venom gland into oesophagus: 0 – into rear part of buccal mass; 1 – into oesophagus behind buccal mass.
16. Number of muscular layers of the muscular bulb: 0–2 layers; 1–3 layers.
17. Orientation of fibres in outer two layers of muscular bulb: 0 – similar orientation; 1 – opposite orientation.
18. Raddula: central 'tooth': 0 – absent; 1 – central ridges present; 2 – spinose tooth.
19. Radula: curved lateral 'teeth': 0 – absent; 1 – present.
20. Radula: marginal teeth: 0 – *Epidirona* type; 1 – *Inquisitor* type; 2 – *Funa* type; 3 – *Haedropleura* type; 4 – *Hindsiclava* type; 5 – *Cheungbeia* type; 6 – *Ptychobela* type.

Character 13. During this study we found several distinct morphologies of the salivary glands. Many species possessed the normal acinous type found in most neogastropods. In some species, *Cheungbeia robusta* and *Burchia spectabilis*. the appearance is of modified acinous (State 1). *Funa jeffreysii* and *Antiguraleus morgani* have glands consisting of single tubes surrounded by acinous cells; this we refer to as acinous tubular (state 2). Simple tubular glands are found in *Haedropleura septangularis* and *Naudedrillia,* these are highly coiled in *C. latizonata* (State 3). Finally, in a number of taxa the salivary glands appear to be made up of a mass of anastomosing tubes (State 4).

Character 14. In most Crassispirinae, the venom gland becomes ciliated and duct-like anterior to the nerve ring.

Character 17. The muscle fibres in the outer two layers of the muscular bulb, may either have the same or differing orientations.

Character 18. Although there is no central tooth to the radula in any of Crassispirinae studied, we did observe in two species some low transverse ridges which cross the ribbon (Fig. 14a). We refer to these as transverse ridges. In the outgroup, *Gemmula deshayesii*, a robust central tooth with a spinose central cusp is present (Fig. 18b).

Character 19. In most crassispirines there are no lateral teeth, but amongst the species we examined, two have paired, low, curved structures which are symmetrical on either side of the mid-line (Figs 11c–d). Maes (1983) referred to these structures as 'soft laterals'. It is uncertain whether these structures are homologous with the lateral teeth found in the Drilliidae or other neogastropods.

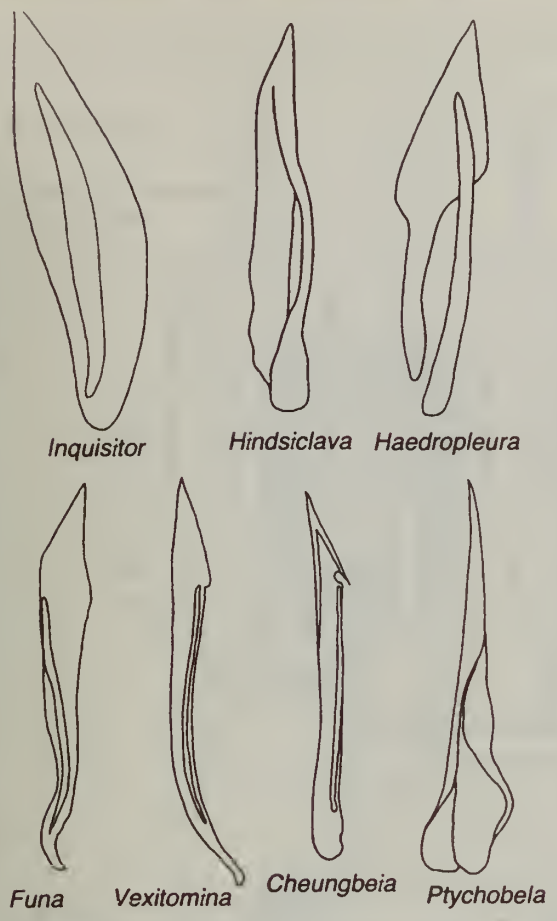

Fig. 31 Summary of major radular types found amongst the Crassispirinae. Not to scale.

They may, as in the Columbellidae (Guralnick & de Maintenon, 1997), be produced by different secretory cells from 'true' teeth.

Character 20: several types of marginal teeth are found within the taxa examined. We have divided these into 6 major types, which are summarized in Fig. 31. The *Epidirona* type (State 0) (Fig. 18a) is a wishbone tooth of the clothes-peg type with the tooth bifurcating into two more or less equal limbs. The *Inquisitor* type (State 1) is the most widely distributed and consists of a robust, pointed, major limb with a smaller, slender, secondary limb attached to it. The *Funa /Vexitomina* type (State 2) consists of a long tooth with a broad, pointed blade and a narrow shaft, with a very thin accessory limb attached to the edge of the shaft. In the *Haedropleura* type (State 3), the major limb has a trowel-like distal end and a narrow shaft, with a slender accessory limb. The *Hindisclava* type (State 4) has a flat, pointed, major limb and a long, slender, detached 'handle-like' accessory limb. The *Cheungbeia* type (State 5) is harpoon-like with a pointed, barbed tip and a straight concave shaft, with a thin splint-like secondary limb attached to the edge of the shaft. Finally, the *Ptychobela type* (State 6) is awl-shaped and hollow, composed of two pieces which are fused along one edge and twisted together.

Outgroup

As the outgroup for the Crassispirinae, we chose *Gemmula deshayesii* from Hong Kong, which has the relatively underived foregut anatomy typical of members of the subfamily Turrinae. Serial sections of the foregut of this species were already available, as well as a published description of the anatomy (Taylor, 1994). The characters of the outgroup are recorded with the Crassispirine species in Table 3.

Table 3 Distribution of character states for the crassispirine gastropods examined. Details of characters listed in Table 2.

Character	1 1 1 1 1 1 1 1 1 1 2 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Crassispira incrassata	2 0 2 0 0 1 0 0 2 0 1 1 0 1 0 1 0 1 0 1
Crassispira maura	1 0 2 0 0 0 0 0 0 0 1 1 0 1 0 1 0 0 0 1
Crassispira dysoni	1 0 2 0 0 0 0 1 3 0 1 1 0 1 0 0 0 0 0 1
Crass. harford. flucki	0 0 0 0 0 1 0 0 3 2 0 1 0 1 0 1 0 0 0 1
Crassispira latizonata	2 1 1 0 1 0 0 1 2 0 0 1 3 1 0 1 0 0 0 1
Crassispira pluto	1 0 0 0 0 0 1 0 1 0 0 1 0 1 0 ? ? 0 0 1
Crassispira kluthi	0 0 1 0 1 2 1 1 2 1 1 1 0 1 0 1 0 0 0 1
Crassispira tepocana	1 0 2 0 1 2 1 1 2 0 1 1 4 1 0 1 0 0 0 1
Crassispira xanti	1 0 2 1 1 2 0 1 0 0 1 1 0 1 0 1 0 0 0 1
Crassispira turricula	2 0 1 1 1 0 0 1 1 2 0 1 4 1 0 1 0 0 1 1
Crassispira apicata	1 0 1 1 0 0 0 0 1 2 0 1 4 1 0 1 0 0 1 1
Hindsiclava andromeda	2 0 2 0 1 2 0 1 1 0 0 1 4 1 0 1 0 ? ? ?
Hindsiclava militaris	2 0 2 1 1 0 0 0 1 0 0 1 4 1 0 1 0 1 0 4
Miraclatlurella bicanal.	1 0 1 0 0 2 0 1 2 1 0 1 0 1 0 1 0 0 0 1
Haedropleura septangularis	1 0 1 1 1 0 0 0 1 0 0 0 3 0 0 1 0 0 0 3
Naudedrillia prateriss.	1 0 0 0 0 2 0 1 2 0 0 1 3 1 0 1 0 0 0 3
Nquma scalpta	1 0 0 0 0 2 0 1 3 1 0 1 4 1 0 1 0 0 0 1
Epidirona gabensis	0 0 2 0 0 0 0 1 3 0 0 1 0 1 1 1 0 0 0 0
Funa latisinuata	1 0 1 1 1 0 1 0 1 1 0 1 1 1 0 1 0 0 0 2
Funa jeffreysii	1 0 1 1 0 0 0 1 1 1 0 1 2 1 0 1 0 0 0 2
Inquisitor latifasciata	1 1 0 0 1 2 1 0 1 1 0 1 1 1 1 0 0 0 0 1
Inquisitor aff. *adenicus*	1 0 1 0 0 0 0 1 3 0 0 1 0 1 0 1 0 0 0 1
Inquisitor aemula	0 0 0 0 0 2 0 1 2 2 0 1 0 1 0 1 0 0 0 1
Ptychobela suturalis	2 1 0 0 1 0 0 1 0 2 0 1 0 1 0 1 0 0 0 6
Cheungbeia mindanensis	2 0 0 0 0 1 0 0 1 0 0 1 0 1 0 1 0 0 0 5
Cheungbeia robusta	1 0 0 0 0 1 0 0 2 0 0 1 1 1 0 1 0 0 0 5
Antiguraleus morganus	1 0 0 0 1 0 0 1 1 0 0 0 2 0 0 1 0 0 0 3
Guraleus costatus	1 0 0 0 1 0 1 1 0 2 0 1 0 1 0 1 0 0 0 1
Burchia spectabilis	2 1 1 0 1 2 1 0 3 0 0 1 1 1 1 0 0 0 0 1
Vexitomina garrardi	1 0 2 0 1 1 0 0 3 0 0 1 0 1 0 1 0 0 0 2
Turridrupa bijubata	1 0 2 0 1 0 0 1 3 0 1 0 0 1 1 0 0 2 0 0
Gemmula deshayesi	0 0 1 0 0 0 0 1 3 2 0 0 0 0 0 1 0 2 0 0

Character distribution

The distribution of the character states amongst the species studied along with those of the outgroup are shown in the data matrix (Table 3). For *Crassispira latizonata* and *Hindsiclava andromeda* we had insufficient material to investigate the radula and there are no published descriptions. In the case of *Crassispira pluto*, the muscular bulb was lost from the sectioned material.

Phylogenetic analysis

This was performed using PAUP version 3.1 and McClade 3.04 for subsequent analysis. Using the data matrix of Table 3 and the heuristic sort option we obtained 24 equally parsimonious trees of 104 steps, with a Consistency Index of 0.33 and Retention Index of 0.54. A consensus tree generated from the 24 trees is shown in Fig. 32a and an example shown in Fig. 32b. Internal nodes of the tree are supported by relatively few characters and there is a high level of homoplasy. *Epidirona gabensis* and *Turridrupa bijubata* are undifferentiated from the outgroup *Gemmula* in all trees. Whilst, *Crassispira dysoni* and *Inquisitor* aff. *adenicus* which both possess *Inquisitor* type teeth, are undifferentiated in the consensus tree but form a weakly supported branch in most trees. Species classified into different subgenera of *Crassispira* appear in widely separated parts of the tree (Fig. 32b), apart from *Crassispira (Crassispira)* s. s. and *Crassispira (Striospira)* which form a monophyletic clade.

Because we sampled only 24 out of the 46 genera and subgenera and because of the large amount of homoplasy, it would be prema-

Fig. 32 a, Consensus tree (50% majority rule) of crassispiran relationships with percentage support indicated on branches. b, Single tree. Species classified in different subgenera of *Crassispira* indicated.

ture to use the tree as a basis for classification of the Crassispirinae. However, foregut characters have potential for unravelling relationships amongst the gastropods with rather similar shells.

DISCUSSION

Summary of anatomical variation in Crassispirinae

Considerable variation was found in the configuration of the foregut amongst the species we studied. This variation is reflected in the fact that we have recognised 13 main types of crassispirine foregut (Figs 33–34), which differ in the presence, position and morphology of the main structures, such as buccal mass, salivary glands, buccal lips and sphincters of the buccal tube.

Several features are characteristic for the vast majority of the crassispirines and these include a glandular lining to the anterior part of the rhynchodeum and the ability of the posterior part of the rhynchodeum to evert during proboscis protraction (except *Crassispira harfordiana flucki* – Fig. 33 C). This is recognised by the continuity of the posterior rhynchodeal and proboscis walls. In nearly all Crassispirinae, the oesophagus is elongated between the

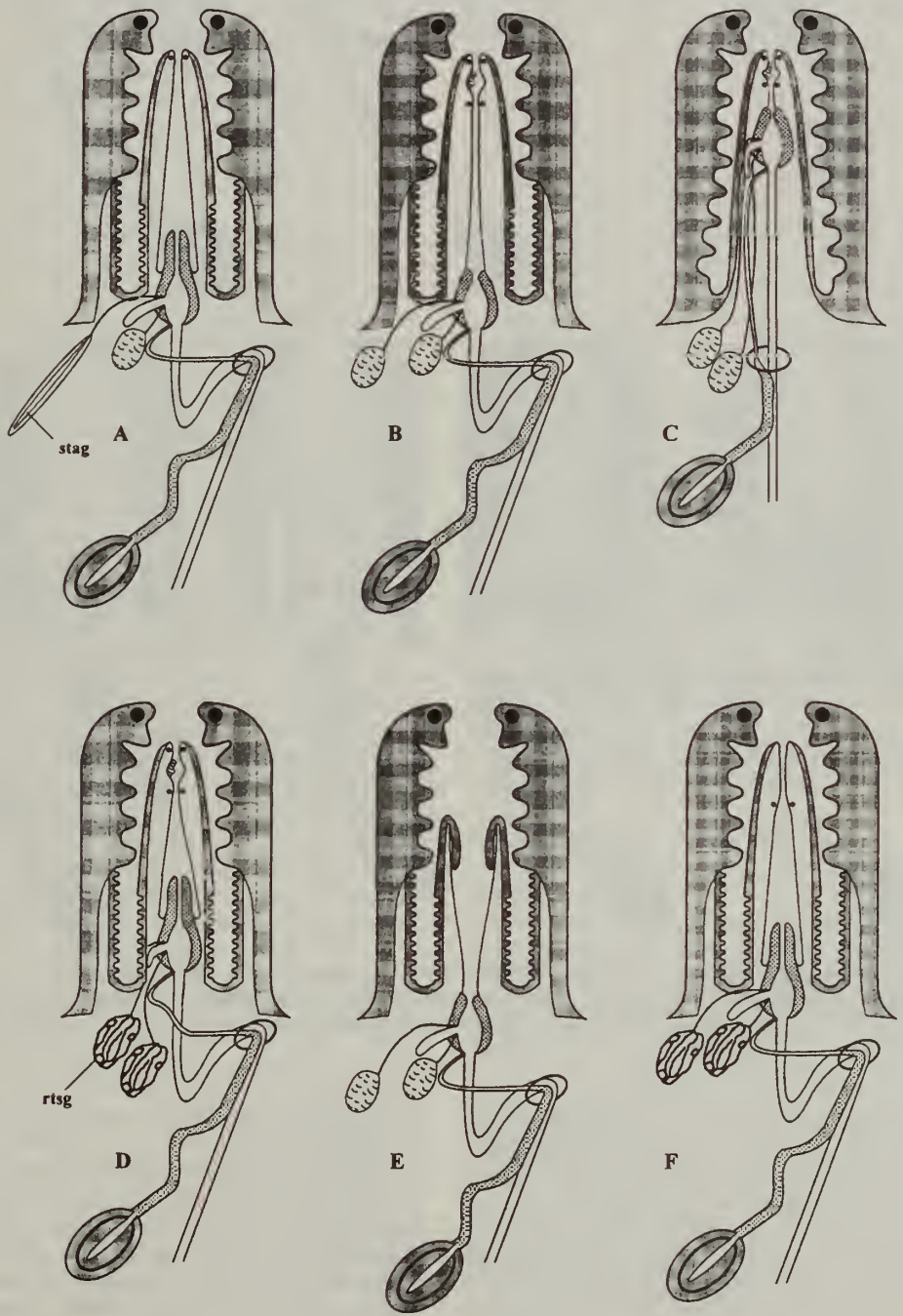

Fig. 33 Diagram summarizing some of the major types of foregut morphology found among the Crassispirinae. Not to scale. A, *Crassispira (Crassispira)* spp. – with acinous salivary glands, *Funa* spp. – with single tube acinous gland. B, *Crassispira (Gibbaspira) dysoni.* C, *Crassispira (Glossispira) harfordiana flucki.* D, *Crassispira (Crassiclava)* spp. E, *Burchia* new species. F, *Crassispira (Striospira) tepocana.*

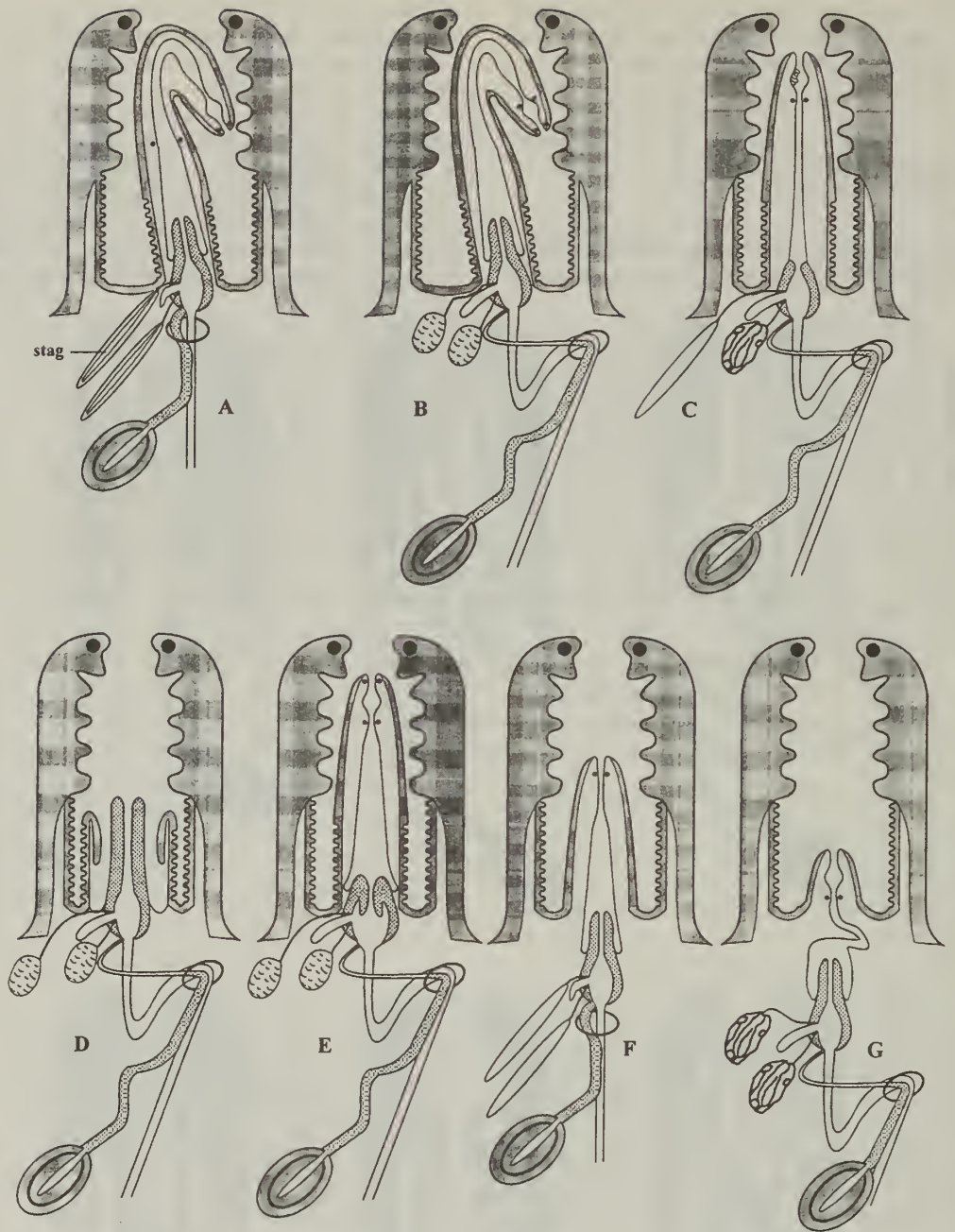

Fig. 34 Diagram summarizing some of the major types of foregut morphology found among the Crassispirinae. Not to scale.
A, *Antiguraleus morganus*. B, *Cheungbeia* spp. C, *Nquma scalpta* (anastomosing tubular salivary glands) and *Naudedrillia praetermissa* (simple tubular salivary glands). D, *Inquisitor latifasciata* and *Ptychobela suturalis* with a retracted proboscis. E, *Ptychobela suturalis* with protracted proboscis. F, *Haedropleura septangularis*. G, *Hindsiclava* spp.

buccal mass and the nerve ring, usually forming a more or less long loop. This character is also associated with the ability to evert the posterior rhynchodeum. Exceptions are *Antiguraleus morganus* (Fig. 34 A) and *Haedropleura septangularis* (Fig. 34 F).

The length of the proboscis in its retracted position is very variable, this is because the posterior part of the rhynchodeum can evert, so that on retraction, the proboscis wall becomes the wall of the rhynchodeum. The most extreme expression of this is found in *Hindsiclava* spp. (Fig. 34 G), where the proboscis, in its retracted position, is extremely short, occupying less that 1/5 of the rhynchocoel length. The anatomy of the posterior part of rhynchodeum suggests that when protracted the proboscis would be similar in length to that of the other species.

Elongation of the oesophagus is coupled with the anterior elongation of the venom gland. This results in the formation of a usually long, muscular, non-glandular duct, which in nearly all the Crassispirinae studied, opens into the posterior part of the buccal mass at the border with the oesophagus. Exceptions are *Antiguraleus morganus* (Fig. 34 A) and *Haedropleura septangularis* (Fig. 34 F), which are the only species lacking the oesophageal loop. In Turriinae (*Turridrupa*) there is modification of the venom gland in front of the nerve ring, but the oesophageal loop is absent.

In many species, there are large buccal lips, which protrude into the buccal tube (eg. Fig. 33 A – *Funa* spp. 33 D – *Crassispira (Crassiclava)* spp.). In several species, for example, *Ptychobela suturalis* (Fig. 34 E) the buccal lips are able to invert inside the buccal cavity. The functional significance of this feature is unknown, but could perhaps be associated with the passage of food items into the buccal cavity.

In four species, the tip of the proboscis is able to invert inside itself (Figs. 33 E, 34 D). In *Burchia spectabilis* (Fig. 33 E), the buccal mass is situated at the base of the proboscis and is not protruded through the mouth, when the proboscis tip is inverted. By contrast, the long buccal lips of *Inquisitor latifasciata* and *Ptychobela suturalis* (Fig. 34 D) are exposed through the mouth when the proboscis tip is inverted. In the latter species, the foregut has a totally different appearance when the proboscis is partially protracted (Fig. 34 E). For one species (*Funa jeffreysii* – Fig.19), it has been demonstrated that the whole buccal mass can be protruded through the mouth opening (Taylor, 1994, fig. 8). It is highly possible, that in other crassispirines the buccal mass may also be protruded through the mouth and used in prey capture.

Many Conoidea possesses one or more sphincters in the anterior part of the buccal tube, these grip the detached, marginal, radular teeth at the proboscis tip (Kantor & Taylor, 1991; Taylor *et al.*, 1993). In Crassispirinae, up to two sphincters were found within the buccal tube (Fig. 33 B – *Crassispira dysoni*, Fig. 33 D – *Crassispira (Crassiclava)*, and others). Where two sphincters were present, the anterior was usually much smaller than the posterior. The positions of the sphincters also vary. A sphincter(s) was defined as anterior in position, if it lies at a distance of not more than 2.5 marginal tooth lengths from the mouth opening. The more posterior sphincter of the buccal tube is shifted backwards in some species, sometimes occupying a position in the mid-proboscis (Fig. 34 A – *Antiguraleus morgani*). If the sphincter lies at a distance of more than 2.5 marginal tooth lengths from the mouth we classified it as intermediate (e.g. *Crassispira dysoni* – Fig. 33 B; *Crassispira (Striospira)* spp. – Fig. 33 F, and others). An intermediate sphincter within the buccal tube has previously been found only in one species of *Splendrillia* (Drilliidae) (Sysoev & Kantor, 1989). Its function is obscure, for it cannot be used for gripping teeth at the proboscis tip, but may perhaps be used in transportation of the tooth from the radular sac to the proboscis tip. The anterior buccal tube sphincter is often absent and only the intermediate sphincter present (*Nquma scalpta, Naudedrillia praetermissa* – Fig. 34 C; *Inquisitor* spp.; *Crassispira (Striospira)* spp. – Fig. 33 F; *Miraclathurella bicanalifera*). Only rarely are both sphincters absent and this indicates that separate marginal teeth are probably not used at the proboscis tip (*Burchia spectabilis* – Fig. 33 E, *Inquisitor latifasciata* – Fig. 33 D).

As in the majority of conoideans, there is in crassispirine species a more or less well-defined, sac-like enlargement of the buccal tube. which is lined with a modified epithelium. The structure is associated with the gripping of single radular teeth at the proboscis tip (Kantor & Taylor, 1991). From our sections of Crassispirinae, it appears that the presence and degree of development of the sac-like enlargement is not correlated with the position of the buccal tube sphincters (either both anterior and intermediate, or only one may be present). In three species, namely, *C. turricula, C. apicata* (Figs 12, 33 D) and *C. dysoni* (Figs 5, 33 B), the walls of the enlargement were more muscular than the rest of the buccal tube. No enlargement was found in *Burchia spectabilis* (Fig. 33 E), *Inquisitor latifasciata* (Fig. 34 D), *C. tepocana* and *C. klutlui* (Fig. 33 F). In the two former species, the proboscis tip is able to invert and the separate teeth are not gripped at the proboscis tip, whilst we have no other information about *C. tepocana* and *C. klutlui*.

An unusual character, previously found only in *Splendrillia* (Sysoev & Kantor, 1989), is the presence of an epithelial pad in the anterior portion of the buccal tube. For some species, marginal teeth were seen adhering to this pad, probably for more secure fixation. The epithelial pad was found in several crassispirine species, for example, *Crassispira (Crassiclava)* species (Fig. 33 D) and *Crassispira dysoni* (Fig. 33 B).

Salivary glands differ greatly in size and histology. Before this study, only two types of salivary glands were recognised amongst the Conoidea – acinous and simple tubular (Taylor *et al.*, 1993). The structure of the glands was thought to be a character useful at subfamilial level, for instance, differentiating the Mangeliinae and Raphitominae. However, amongst the crassispirines we were able to recognise four types of salivary gland. Besides the acinous salivary glands (found in majority of species) and simple tubular glands (*Haedropleura septangularis* – Fig. 34 F; *Naudedrillia praetermissa* – Fig. 34 C), we found anastomosing tubular (Figs 33 D, F; 34 C,G) and glands consisting of a simple tube surrounded by acinous cells (*Funa* spp. – Fig. 33 A; *Antiguraleus morganus* – Fig. 34 A). Sometimes, species attributed to the same genus and even subgenus possess different types of glands. For example, in *Crassispira (Striospira) tepocana,* the glands are anastomosing tubular, while in *C. (S.) klutlui* and *C.(S.) xanthi* they are acinous. Moreover, it should be emphasised, that there were no correlations between the structure of the glands and the foregut anatomy. Sometimes in species possessing the same type of foregut, the glands were of different histology (eg. *Nquma scalpta* and *Naudedrillia praetermissa* – Fig. 34 C; and *Crassispira (Crassispira)* spp. and *Funa* spp. – Fig. 33 A).

The Crassispirinae is the only subfamily of the Conoidea, in which a variety of salivary glands has so far been recorded. It is still unclear whether the simple tubular salivary glands can be derived from the acinous type. However, recently, it has been demonstrated (Ball, Taylor & Andrews, in press) that in the embryonic development of *Nucella,* the salivary ducts are formed first, and the salivary gland itself appears later at the tip of the duct. From this, it can be suggested that the simple tubular glands may represent the enlarged ducts, while the gland itself was not developed. Thus, the simple tubular salivary glands may originate from the acinous by paedomorphosis. This may also explain the origin of the anastomosing tubular glands, which could possibly be the result of extensive coiling of the initial duct.

Shell and radular characters

Radula

Radular morphology has been used extensively to recognise and classify suprageneric categories within the Conoidea (e.g. Powell, 1966; McLean, 1971; Kilburn, 1988, Taylor *et al.*, 1993). However, this study has demonstrated that within the Crassispirinae, there is no great congruence between radular and anatomical characters.

Many crassispirine taxa have quite similar radular teeth (e.g. Figs 4, 11) with the wishbone tooth formed by a robust, pointed, major element and a smaller, more slender, secondary element. However, this similarity of radula morphology is not reflected in foregut anatomy and taxa with the same type of teeth often have widely different arrangements of the foregut; for example *Inquisitor latifasciata* (Figs 17b, 20) and *Crassispira harfordiana flucki* (Figs 4d, 6). In other cases, some gastropods possess rather similar and distinctive foregut anatomies, as for example, *Inquisitor latifasciata* and *Ptychobela suturalis*. However, they have very different radular morphologies, with *I. latifasciata* having the rather standard crassispirine wishbone form, but *P. suturalis* has the autapomorphic, awl-shaped, hollow teeth (Fig. 23a).

Although teeth with the wishbone form are found in the subfamilies Turrinae, Clavatulinae and Cochlespirinae, most variation and the most extreme forms are found within taxa classified as Crassispirinae. Although rather a disparate range of radular teeth was found amongst the species we studied, all can probably be derived from the basic wishbone form. Thus, the derivation of the rather extreme forms of wishbone teeth seen in *Hindsiclava* and *Haedropleura* can be envisaged by changes in the relative proportion of the elements. In the large, paddle-shaped teeth of *Funa* and *Vexitomina,* a thin, splint-like secondary limb lies along the shaft of the main tooth. In the most-derived, harpoon-like teeth of *Cheungbeia*, a similar small splint-like secondary limb lies along the edge of the shaft. Finally, the hollow awl-shaped teeth of *Ptychobela* consist of two components and can probably be derived from flattening and fusing of the two wishbone components.

Congruence of shell characters

Shell characters are also a rather poorly correlated with radular morphology or characters of foregut anatomy. A good example of this problem is seen in the genera *Inquisitor*, *Funa*, and *Ptychobela.* These have rather similar shells but the radulae are quite different, *Inquisitor* having the standard crassispirine wishbone form, *Funa* has bladed, paddle-shaped teeth and *Ptychobela* possesses awl-shaped hollow teeth. The allocation of shells to these genera is difficult without radular evidence and many species have been rather arbitrarily assigned to genera (e.g. Wells, 1994).

A striking example of the similarity of shell characters in different families is seen between the pairs of West American species *Crassispira (Striospira) tepocana* (see Keen, 1971 fig. 1701) and *Strictispira ericana* (Keen, 1971 fig. 1727) and *C. (Striospira) xanti* (Keen, 1971 fig. 1702) with *Strictispira stillmani* (Keen, 1971 fig. 1728). These pairs of similar gastropods have quite different anatomies. The *Strictispira* species (family Strictispiridae) lack the venom gland, have the buccal mass located at the proboscis tip and possess very distinctive radula teeth (Kantor & Taylor, 1994).

Parallel evolution of hypodermic feeding mechanism

In two genera, the radular teeth are quite different from the rest of the Crassispirinae, which for the most part consist of variations on the robust wishbone form. In *Cheungbeia* species, the teeth are long, slender and harpoon-like, with distal barbs, whilst in *Ptychobela* the teeth are pointed, awl shaped and hollow. Although most conoidean teeth, including the wishbone types can be used at the proboscis tip for the penetration of prey, the hollow, barbed teeth are regarded as the more efficient. Taylor *et al.* (1993) demonstrated that hollow, barbed teeth had evolved several times within the Conoidea and these two taxa may represent further evolutionary pathways to the hypodermic feeding mechanism. The teeth in *Cheungbeia* and *Ptychobela* although quite different in morphology can both be derived from the crassispiran wishbone form. Although *Cheungbeia* is long and gutter-shaped, a small and very thin accessory limb lies along one side of the shaft (Fig. 26). A similar reduction in the size of the accessory limb is seen in *Funa* and *Vexitomina* which have paddle-shaped teeth, with the thin secondary limb lying along the shaft (Figs 23 b–d). In *Ptychobela,* each tooth is formed from two more or less equal parts which are fused along one edge and loosely enrolled. Neither of these two tooth types can be considered as precursors of the enrolled barbed teeth found in *Conus* (Coninae, sensu Taylor *et al.* 1993) because their foregut anatomy is different. Both *Cheungbeia* and *Ptychobela,* for example, have the modified epithelium of the rhynchodeum, the elongated oesophagus, and the modified venom gland. None of these features is found in *Conus*. Moreover, Conidae have lost the radular membrane and possess a radular caecum for the storage of teeth prior to use.

Comparison between conoidean subfamilies

Three other subfamilies within the Turridae, the Turrinae, Clavatulinae and Cochlespirinae possess the wishbone type of radular teeth and their features should be compared with those of the Crassispirinae.

Members of the Turrinae have wishbone teeth which differ in morphology from those of the other taxa. The proximal half of each tooth is divided like a clothes-peg into two more or less equal units (Fig. 18), with the limbs not detached. This contrasts with the wishbone teeth in the other subfamilies which have the limbs unequal in size and thickness and the secondary limb not in structural continuity with the major limb. Some species of Turrinae also have a quadrate central tooth with a spine-like central cusp. Species of Turrinae also differ in a number of anatomical characters; there is usually no elongation of the oesophagus, no change in the histology of the venom gland anterior of the nerve ring and the rhynchodeum is uniformly glandular along its length (Taylor *et al.*, 1993; Taylor, 1994).

The Clavatulinae have wishbone teeth with a large, bladed, major limb and the secondary limb inserted into a 'V' shaped groove. Additionally, central teeth are usually present. They also have a medio-lateral nucleus to the operculum rather than the terminal position found in the other turrid subfamilies. The buccal mass often lies within the proboscis, but as in Crassispirinae, the oesophagus is often elongated between the nerve ring and buccal mass and the venom gland changes to a ciliated duct anterior to the nerve ring (Kantor, 1990; Taylor *et al.*, 1993).

The Cochlespirinae, represented by *Aforia*, *Antiplanes*, and *Cochlespira*, have similar wishbone teeth to the Crassispirinae, with some species possessing a central tooth, and some having plate-like lateral teeth (Sysoev & Kantor, 1987, 1988; Kantor & Sysoev, 1991). In *Cochlespira* and *Aforia*, the venom gland joins the oesophagus some way to the posterior of the buccal mass, but no details are available for other taxa.

We have found a great variation in the structure of the foregut in the Crassispirinae and some of these features are shared with the Turrinae, Clavatulinae and Cochlespirinae. However, rather few species have been studied from the latter three groups compared with the more extensive survey of the Crassispirinae. A reappraisal of the boundaries and relationships of these four subfamilies is required, but this cannot be attempted before more anatomical details are available from a much wider range of taxa.

Systematic conclusions

ANTIGURALEUS and associated genera

On the basis of his study of southern African species, Kilburn (1994) suggested that two genera, *Anacithara* and *Antiguraleus,* which had previously been referred to the subfamily Mangeliinae (as in Powell, 1966), should be transferred to the Crassispirinae on the basis of radular characters. We studied one of the South African species, *Antiguraleus morgani* and confirm that it has a crassispirine type of radula (Fig. 28a) and also has many foregut characters consistent with other members of the Crassispirinae. Additionally, we also sectioned the eastern Australian species, *Guraleus costatus*, and this also has an operculum, with a radula and foregut anatomy of the

Crassispirinae (Fig. 28b). However, another Australian species that we sectioned, *Antiguraleus howelli* (Laseron), possesses a typical mangeliinae anatomy and Powell (1966, fig. 138) also illustrates a typical mangeliine radula for *Antiguraleus murrheus* (Webster, 1906). Our observations suggest that the mostly Australasian species, currently assigned to the *Guraleus* group of genera (*Antiguraleus*, *Paraguraleus*, *Guraleus* and *Neoguraleus*) (Powell, 1966) represent at least two different subfamilies, and the whole complex is in great need of critical revision.

EPIDIRONA

This genus was assigned to the Crassispirinae by Sysoev (In: Taylor *et al.*, 1993) on the evidence of the radula of the type species *Epidirona hedleyi* Iredale, 1931, which has teeth with the wishbone form similar to many other species in the subfamily, with a robust, pointed, major limb and a slender secondary limb (Powell, 1964, plate 229; Powell, 1966, fig. 33). However, our studies show that *Epidirona gabensis* has a radula with the wishbone teeth with the form typical of the subfamily Turrinae, i.e. awl shaped and bifurcating in the proximal half (Fig. 18) . Similar teeth were illustrated by Powell (1966, fig. 32) for *Epidirona nodulosa* Laseron, 1954. In our phylogenetic analysis *Epidirona gabensis* was shown to be more similar, despite some anatomical differences, to the outgroup *Gemmula deshayesii,* rather than to the crassispirine species. However, the type species, *Epidirona hedleyi* would seem to be a crassispirine on the evidence of the radula, but we have no anatomical information to confirm this.

Our conclusions are that *Epidirona gabensis* and *E. nodulosa* should be classified within the subfamily Turrinae. *Epidirona hedleyi*, the type species, is likely to be a crassispirine and reference to the illustrations in Powell (1964, plate 230) shows that it differs from the other species on shell characters. A new generic name is necessary for the *Epidirona* species which possess the Turrinae-type of radular teeth, however, anatomical or at least radular studies of the other species is desirable.

TURRIDRUPA

The systematic position of this genus has been uncertain. Powell (1966; 1967) referred it to the Turrinae on shell characters, but his illustration (1967 fig. 300) of the radula of *T. jubata* would seem to be a misinterpretation. Subsequently, Kilburn (1983) transferred *Turridrupa* to the Clavinae (= Drilliidae), but later, on the basis of radular characters (*Turridrupa bijubata* and *cincta*) concluded (1988 p. 235) that *Turridrupa* was 'a primitive crassispirine clade.'. Additionally, one of the species, *Turridrupa cerithina,* was again on radular characters, transferred to the genus *Inquisitor,* (Kilburn, 1988, p. 267). Unfortunately, the anatomy is known only for *Turridrupa bijubata* which has a quadrate central tooth and wishbone marginals (Kilburn, 1988 fig. 40) which are of the clothes-peg type similar to those of the Turrinae. Also, our phylogenetic analysis shows that in anatomical characters, *Turridrupa bijubata* is more similar to the outgroup *Gemmula* (Turrinae) and to *Epidirona gabensis* than any of the Crassispirinae. We have not studied *Turridrupa cerithina* which has a different shell morphology from other species and may well be a crassispirinan. In conclusion, we think that *Turridrupa* should be classified in the Turrinae, with *T. cerithina* possibly in the Crassispirinae.

CRASSISPIRA and subgenera

At present. the genus *Crassispira* is usually divided into eight subgenera. Our phylogenetic analysis shows that *Crassispira (Crassispira)* and *C. (Striospira)* form a monophyletic clade, but species of the other subgenera appear at widely separated positions on the cladogram (Fig. 33) and have different anatomies from *Crassispira* s.s. Our results suggest that the subgenera of *Crassispira* should be raised to full generic status, with perhaps a case for the retention of *Striospira* as a subgenus.

CONCLUSIONS

This detailed study of the anterior alimentary system of one subfamily of conoideans has revealed an extraordinary diversity of foregut configuration. It is uncertain whether so much variation exists in other conoidean groups, for far fewer species have been studied. However, preliminary evidence suggests that a similar diversity of foreguts exists in the Raphitominae, Clavatulinae and Terebridae (Taylor, 1990; Taylor *et al.*, 1993; Sysoev & Kantor, 1995; Kantor & Sysoev, 1996). The anatomy of *Conus* has usually been taken as being typical of the whole Conoidea, but its foregut is in many ways rather underived (basal buccal mass, unmodified rhynchodeal wall, no oesophageal loop, unmodified anterior venom gland). In fact, *Conus* can be regarded as just one of many possible foregut configurations found within the Conoidea. Virtually all the organs of the foregut can vary in presence or absence, size and position. Thus for example, the proboscis may be very long or very short; the buccal mass may be situated near the tip of the proboscis, at the base or to the posterior; much of the posterior rhynchodeum may be able to evert thus forming an extended proboscis, or there may be several of no sphincters in the buccal tube. Indeed, more extreme conditions exist in the some species of Raphitominae and Terebridae, where the venom gland, radula, salivary glands and proboscis have been lost. This diversity of foregut structure of conoideans likely reflects considerable variation in feeding behaviour and methods of prey capture. Unfortunately, apart from *Conus*, few details are available for other conoidean taxa (Miller, 1989; Taylor *et al.*, 1993).

ACKNOWLEDGEMENTS. We are grateful to Gary Rosenberg, Dick Kilburn, Jim McLean, Philippe Bouchet, Ian Loch, Winston Ponder, Graham Oliver and Marco Oliverio for the generous donation of some of the specimens used in this study. Alexander Sysoev provided discussion and encouragement. Brian Morton gave much logistic support for the collection of specimens in Hong Kong. David Cooper expertly prepared many of the serial sections. Yuri Kantor is grateful to the Royal Society for the air fare enabling him work in London.

REFERENCES

Ball, A.D., Taylor, J.D. & Andrews, E.B. 1997. Development of the acinous and accessory salivary glands in *Nucella lapillus* (Neogastropoda: Muricoidea). *Journal of Molluscan Studies* **63**: 245–260.

Fernandes, F., Rolán, E. & Otero-Schmitt, J. 1995. The genus *Crassispira* (Gastropoda, Turridae) in West Africa. *Journal of Conchology* **35**: 283–301.

Guralnick, R. & de Maintenon, M. 1997. Formation and homology of radular teeth; a case study using columbellid gastropods (Neogastropoda: Columbellidae). *Journal of Molluscan Studies*, **63**: 65–77.

Kantor, Y.I. 1990. Anatomical basis for the origin and evolution of the toxoglossan mode of feeding. Malacologia, **32:** 3–18.

Kantor, Y.I. & Sysoev, A.V. 1991. Mollusks of the genus *Antiplanes* (Gastropoda: Turridae) of the northwestern Pacific Ocean. *Nautilus* **105**: 119–146.

Kantor, Y.I. & Sysoev, A.V. 1996. New data on the foregut morphology of Raphitominae (Conoidei, Conidae). *Ruthenica* **5**: 155–157.

Kantor, Y.I. & Taylor, J.D. 1991. Evolution of the toxoglossan feeding mechanism: new information on the use of the radula. *Journal of Molluscan Studies* **57**: 129–134.

Kantor, Y.I. & Taylor, J.D. 1994. The foregut anatomy of *Strictispira paxillus* (Reeve, 1845) (Conoidea: Strictispiridae). *Journal of Molluscan Studies* **60**: 343–346.

Keen, M.A. 1971. *Sea shells of tropical West America*. 2nd edition. Stanford University Press, Stanford, California

Kilburn, R.N. 1983. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 1. Subfamily Turrinae. *Annals of the Natal Museum* **25**: 549–585.

Kilburn, R.N. 1988. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 4. Subfamilies Drilliinae, Crassispirinae and Strictispirinae. *Annals of the Natal Museum* **29**: 167–320.

Kilburn, R.N. 1989. Notes on *Ptychobela* and *Brachytoma*, with the description of a new species from Mozambique (Mollusca: Gastropoda: Turridae). *Annals of the Natal Museum* **30**: 185–196.

Kilburn, R.N. 1994. Turridae[s./l.] (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 7. Subfamily Crassispirinae, section 2. *Annals of the Natal Museum* **35**: 177–228.

McLean, J.H. 1971. A revised classification of the family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific. *Veliger* **14**: 114–130.

Maes, V.O. 1983. Observations on the systematics and biology of a turrid assemblage in the British Virgin Islands. *Bulletin of Marine Science* **33**: 305–3.

Miller, J.A. 1989. The toxoglossan proboscis: structure and function. *Journal of Molluscan Studies* **55**: 167–182.

Powell, A.W.B. 1964. The family Turridae in the Indo-Pacific. Part 1. The subfamily Turrinae. *Indo-Pacific Mollusca* **1**: 227–346.

Powell, A.W.B. 1966. The molluscan families Speightiidae and Turridae. An evaluation of the valid taxa, both Recent and fossil, with lists of characteristic species. *Bulletin of the Auckland Institute and Museum* **5**: 1–184.

Sheridan, R., van Mol J.J. & Bouillon, J. 1973. Etude morphologique du tube digestif de quelques Turridae de la région de Roscoff. *Cahiers de Biologie Marine* **14**: 159–188.

Sysoev, A.V. 1996. Deep-sea conoidean gastropods collected by the John Murray Expedition, 1933–34. *Bulletin of The Natural History Museum, London (Zoology)* **62**: 1–30.

Sysoev, A.V. & Kantor, Y.I. 1987. Deep-sea gastropods of the genus *Aforia* (Turridae) of the Pacific: species composition, systematics, and functional morphology of the digestive system. *Veliger* **30**: 105–126.

Sysoev, A.V. & Kantor, Y.I. 1988. Three new deep-sea molluscs of the genus *Aforia* (Gastropoda: Toxoglossa: Turridae). *Apex* **3**: 39–46.

Sysoev, A.V. & Kantor, Y.I. 1989. Anatomy of molluscs of genus *Splendrillia* (Gastropoda: Toxoglossa: Turridae) with description of two new bathyal species of the genus from New Zealand. *New Zealand Journal of Zoology* **16**: 205–214.

Sysoev, A.V. & Kantor, Y.I. 1995. Two new species of *Phymorhynchus* (Gastropoda, Conoidea, Conidae) from the hydrothermal vents. *Ruthenica* **5**: 17–26.

Sysoev, A.V. & Taylor, J.D. 1997. A new species of crassispirine gastropod from the Houtman Abrolhos Islands, Western Australia (Gastropoda, Conoidea, Crassispirinae). *Bulletin of the Natural History Museum London* (Zoology) **63**: 51–53.

Taylor, J.D. 1990. The anatomy of the foregut and relationships in the Terebridae. *Malacologia* **32**: 19–34.

Taylor, J.D. 1994. Foregut anatomy of the larger species of Turrinae, Clavatulinae and Crassispirinae (Gastropoda: Conoidea) from Hong Kong. pp.185–212. *In*: Morton B. (ed.) *The Malacofauna of Hong Kong and Southern China III*. Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China. Hong Kong University Press, Hong Kong.

Taylor, J.D., Kantor, Y.I. & Sysoev, A.V. 1983. Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (= Toxoglossa) (Gastropoda). *Bulletin of the Natural History Museum London (Zoology)* **59**: 125–170.

Taylor, J.D. & Wells, F.E. 1994. A revision of the crassispirine gastropods from Hong Kong (Gastropoda: Turridae). pp.101–116. *In*: Morton, B. (ed.) *The Malacofauna of Hong Kong and Southern China III*. Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong University Press, Hong Kong.

Wells, F.E. 1994. A revision of the Recent Australian species of the turrid genera *Inquisitor* and *Ptychobela*. *Molluscan Research* **15**: 71–102.